SIGNIFICANCE OF SELECTIVE PREDATION AND DEVELOPMENT OF PREY PROTECTION MEASURES FOR JUVENILE SALMONIDS IN THE COLUMBIA AND SNAKE RIVER RESERVOIRS

Annual Progress Report

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Edited by

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EXECUTIVE SUMMARY

This document is the 1991 annual report of progress for the Bonneville Power Administration (BPA) research Project No. 82-003 conducted by the U.S. Fish and Wildlife Service (FWS). Our approach was to present the progress achieved during 1991 in a series of separate reports for each major project task. Each report is prepared in the format of a scientific paper and is able to stand alone, whatever the state of progress or completion.

This project has two major goals. One is to understand the significance of selective predation and prey vulnerability by determining if substandard juvenile salmonids (dead, injured, stressed, diseased, or naive) are more vulnerable to predation by northern squawfish, _Ptychocheilus oregonensis_ than standard or normal juvenile salmonids. The second goal is to develop and test prey protection measures to control predation on juvenile salmonids by reducing predator-smolt encounters or predator capture efficiency.

The following point summary gives the major results for 1991 on each of the major project objectives and tasks:

(1) We conducted laboratory experiments to determine whether northern squawfish will ingest dead salmon, and in what proportion if live salmon are also available. When offered equal numbers of live and dead juvenile chinook salmon _Oncorhynchus tshawytscha_, northern squawfish consumed significantly more ($p < 0.01$) dead than live individuals, both in 1400-L circular tanks and in a 11,300-L flowing-water raceway (62% and 79% dead prey consumed, respectively). Estimates of mortality of juvenile salmonids in the Columbia River due to northern squawfish predation have not accounted for consumption of dead salmon; our experiments indicate this probably occurs, and thus the impact of northern squawfish predation on salmonid populations may be less than previously assumed.

(2) We also conducted field experiments in the Bonneville Dam tailrace (Columbia River) to compare predation rates by northern squawfish on live and dead juvenile salmonids. Known numbers of coded-wire tagged live and dead chinook salmon were released into the tailrace on six nights, northern squawfish were collected after each release, and predator stomach contents were examined for prey tags.

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When 50% of salmon released were dead, northern squawfish consumed 60% dead salmon and large northern squawfish (>300 mm fork length) captured relatively more dead salmon than small predators. When 10% of salmon released were dead, 22% of the tags in predator's guts were from dead salmon. These results corroborate laboratory studies and suggest that salmonid losses to northern squawfish below dams should be re-evaluated.

(3) The passage of juvenile salmonids through dams often results in damage to the skin, scale, and slime complex. We conducted laboratory experiments to determine if salmonids descaled on 10% or 20% of their total body area are more vulnerable to predation by northern squawfish. When offered equal numbers of control and descaled juvenile chinook salmon, northern squawfish did not consume significantly ($P < 0.05$) more of either prey type. At the 10% and 20% descaling levels, 48 to 51% and 49 to 60% descaled prey were consumed, respectively. Our results indicate that descaling at low levels does not increase vulnerability of juvenile salmonids to predation.

(4) When equal numbers of stressed and unstressed juvenile spring chinook salmon were exposed to predation by northern squawfish for various lengths of time (1-24 h), only fish receiving an agitation stress and exposed to predation for 1 h showed a significant difference in their vulnerability to predation. The results suggest that there are several aspects to consider in the conduct and interpretation of predation tests designed to assess the effects of stress. Observed responses are likely polymorphic and dependent on the stressor itself, the predator-prey system being studied, and experimental protocols.

(5) We determined the prolonged swimming performance of two sizes of northern squawfish at 12 and 18°C. Swimming performance was positively related to fish size and water temperature. For medium size fish (30-39 cm fork length), the velocity at which 50% of the fish fatigued (FV50) ranged from 95-105 cm/s and maximum performance from 107-112 cm/s. For large fish (40-49 cm), FV50 ranged from 100-114 cm/s and maximum performance from 118-135 cm/s. Our results suggest that high water velocity areas may be

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used to exclude or reduce predation by northern squawfish around juvenile salmonid bypass outlets at Columbia River dams, especially during spring and early summer.

(6) Little is known about northern squawfish reproduction and early life history in the Columbia River. Therefore, we initiated a small-scale study consisting primarily of literature searches and preliminary field and laboratory investigations. Limited sampling was conducted for northern squawfish eggs and larvae in shallow littoral areas of the upper Bonneville pool and the mouth of the Deschutes River. Northern squawfish larvae were cultured in the laboratory, to obtain a developmental series for identification purposes. Additionally, data and curated samples collected during previous ichthyoplankton studies and substrate map information were examined to locate possible spawning locations of northern squawfish.

(7) Northern squawfish were fed (ad libitum) juvenile salmonids using a normal light cycle and with increased light at night, to simulate illumination near dams. The capture rate of salmon by northern squawfish was inversely related to light intensity. Feeding rates were lowest at high light intensities (20 and 0.2 ft-candles), intermediate when light was intermediate (0.015 ft candles), and highest during low-light (<0.001 ft-candles) periods. Increasing the intensity of light during the night resulted in significantly fewer salmon captured by northern squawfish.

Predation by Northern Squawfish on Live versus Dead Juvenile Salmonids

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Abstract

Northern squawfish <u>Ptychocheilus oreaonensis</u> are major predatorsof juvenile Pacific salmonids <u>Oncorhynchus</u> spp. migrating downstream through the Columbia River. Since much of this predation occurs just below the dams, northern squawfish may be preferentially consuming salmonids killed or injured during dam passage. We conducted laboratory experiments to determine whether northern squawfish will ingest dead salmon, and in what proportion if live salmon are also available. When offered equal numbers of live and dead juvenile chinook salmon Q. <u>tshawytscha,</u> northern squawfish consumed significantly more ($P<0.01$) dead than live individuals, both in 1400-L circular tanks and in a 11,300-L flowing-water raceway (62% and 79% dead prey consumed, respectively). If live and dead juvenile chinook salmon were available in proportions more similar to below dams, 20% dead and 80% live, then northern squawfish still significantly selected for dead prey, consuming 36% dead juvenile salmon in both the circular tanks and the raceway. The above experiments were conducted in a natural photoperiod with both light and dark periods. Additional experiments were conducted offering northern squawfish 20% dead juvenile salmon in either 4 h of light or 4 h of dark; northern squawfish were much more selective for dead salmon during bright light (88% of consumed salmon were dead) than during darkness (31% dead consumed). Estimates of mortality of juvenile salmonids in the Columbia River due to northern

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squawfish predation have not accounted for consumption of dead
salmon; our experiments indicate this probably occurs, and thus
the impact of northern squawfish predation on salmonid
populations may be less than previously assumed.

Introduction

The development of hydroelectric power has caused the decline of
anadromous Pacific salmonid Oncorhynchus spp. populations in the
Columbia River for a variety of reasons (Raymond 1968; 1988).
Juvenile mortality during downstream migration has increased due
to injuries from passage through dams; Schoeneman et al. (1961)
reported 11% mortality of juvenile salmonids passing through
turbines and 2% through spillways at McNary Dam on the Columbia
River. Predation is more intense near dams due to higher
densities of predators and juvenile salmonids (Sims et al. 1981;
Vigg 1988; Beamesderfer and Rieman 1991). A dominant predator is
the northern squawfish Ptychocheilus oregonensis, estimated by
Rieman et al. (1991) to have ingested 11% of all juvenile
salmonids entering John Day Reservoir during 1983-1986. Twenty-
six percent of this loss was in the boat-restricted-zone, a 0.5
km^2 area immediately below McNary Dam that is only 0.25% of the
total reservoir area (Rieman et al. 1991).

  If northern squawfish feed on dead or moribund juvenile
salmonids, then mortality due to predation may be less than
previously estimated. The proportions of live, moribund, and dead
juvenile salmonids consumed by northern squawfish in John Day
Reservoir are unknown since the condition of prey at the time of
capture could not be determined from gut samples (Poe et al.
1991). The high density of northern squawfish below McNary Dam
(Beamesderfer and Rieman 1991) could be due in part to a
preference for dead or injured prey. Predators may capture higher
than expected proportions of weaker individuals from prey
populations (Coutant et al. 1979; Temple 1987), although such
differential predation may be more a result of differences in
prey vulnerability than predator selection. The objective of
our study was to determine whether northern squawfish consume
dead juvenile salmonids, and, if so, in what proportion when
offered both live and dead individuals.

Methods

Fish collection and maintenance.-- .Northern squawfish (432.6 mm fork length, FL; SD 36.1; n = 70) were collected from the Columbia River by boat electroshocking and acclimated for at least three weeks in indoor 1400-L circular tanks at approximately river temperatures, 15-17℃. Northern squawfish were fed a maintenance diet of live juvenile coho salmon <u>Oncorhynchus</u> <u>kisutch</u> (80-120 mm FL) during acclimation and between experiments.

Juvenile chinook salmon Q. <u>tshawytschg</u> (80-110 mm FL) were used as prey fish for experiments. Coho and chinook salmon were obtained from the Little White Salmon National Fish Hatchery Complex and held at a maximum density of 2 fish/L in outdoor, 1400-L circular tanks. Salmon were fed a diet of 2.5 mm commercial moist pellets. Tanks received flow-through well water at 6-8°C; juvenile salmonids were not maintained for long periods at higher experimental temperatures because their health deteriorated. Most salmon were acclimated to experimental temperatures for 3 d before a trial began. Due to space constraints, during one set of trials (circular tanks using 50% dead prey) prey were acclimated to higher temperatures an hour prior to experimental initiation.

<u>Experimental systems</u>.-- Experiments were conducted in two indoor fiberglass tank systems. The first system was a series of six 1400-L circular tanks (1.5 m diameter, 0.8 m deep). A recirculating water system supplied each tank with 20 L/min of filtered, ultraviolet light-sterilized well water (Lucchetti and Gray 1988). Temperature was maintained at 15-17°C with an in-line heater. A natural photoperiod was simulated using timers to control a series of flourescent and incandescent lights (15 h light: 9 h dark).

We additionally conducted experiments in a 11,300-L flowing-water raceway (7.6 m long x 1.2 m wide x 1.2 m deep). A centrifugal pump (1700 L/min) recirculated water flow and an electric heater maintained water temperature at 17-18℃. Because northern squawfish in the field are typically found in areas with flows less than 70 cm/s (Faler et al. 1988), flow in the raceway was kept at a low velocity. Flow velocity varied spatially, ranging from about 73 cm/s mid-upstream to 3 cm/s near the downstream bottom Five incandescent lights controlled by a timer simulated ambient photoperiod (15 h light: 9 h dark).

<u>Proportions of available dead prev</u> -- Experiments were conducted in both the circular tanks and the raceway to assess

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northern squawfish predation on juvenile chinook salmon when 20% and 50% of available prey were dead. Prey for the dead groups were killed by blows to the head shortly before an experiment and given adipose fin clips to separate them from live prey that might die during a trial. After being placed into tanks, all dead chinook salmon slowly sank and moved near the bottom with water movements.   Live chinook salmon swam throughout the tanks and often formed schools.

In the six circular tanks, three northern squawfish per tank were used. Three experiments in the six tank system (18 trials) were conducted using 50% dead juvenile chinook salmon, and two experiments (12 trials) were conducted using 20% dead chinook salmon. Northern squawfish were starved for 2-3 d prior to an experiment. A total of 60 chinook salmon were then placed into each tank in the morning; 24 h later, uneaten prey were collected and counted. For the 50% dead trials, 30 live and 30 dead prey (87.7 mm SL; SD 9.3; n = 30) were placed simultaneously into each tank, and for the 20% dead trials, 48 live and 12 dead prey (86.0 mm SL; SD 8.4; n = 30) were used. Prey number was based on maximum daily consumption rates presented by Vigg and Burley (1989).

In the raceway, three trials were conducted at each percentage of available dead prey (20% and 50%). The raceway held ten northern squawfish, which were used for an experiment after a minimum 10-d acclimation period and a 2-d starvation period. Experiments were conducted during 3-h evening intervals (2000-2300 h; with the first 0.5 h light, and the remaining time dark). At the beginning of an experiment, a total of 100 chinook salmon were placed simultaneously into the raceway at the upstream end; for the 20% dead experiments, 20 dead and 80 live prey (86.9 mm FL; SD 6.6; n = 30) were used, and for 50% dead, 50 dead and 50 live prey (107.2 mm FL; SD 6.8; n = 30) were used. Uneaten salmon were removed and counted at the end of the experimental period.

__Pr   in   .   -_____ - Experiments were conducted in five or six circular tanks to determine if predation by northern squawfish on 20% available dead salmon differed between light (215-270 lux) and dark (<0.01 lux) periods. Light experiments were conducted at 0900-1300 on four occasions (22 trials), and dark experiments were conducted at 1800-2200 on five occasions (27 trials). Three northern squawfish per tank were used after a 1-2 d starvation period. Three dead and 12 live juvenile chinook salmon (91.3 mm FL; SD 9.4; n = 30) were placed simultaneously into each tank at the

<u>Data analysis</u>.-- Tanks in which greater than 50% of the prey were consumed were not included in analyses. Trial results were combined for each of the six experiment types (Table 1). Observed and expected frequencies of live and dead prey consumed were compared with a chi-square (X^2) goodness-of- fit test. Expected frequencies, assuming no selection, were 1:4 (20% dead prey) and 1:1 (50% dead prey) ratios of dead versus live consumed salmon.

Results

In all trials (n = 85), only five tanks had greater than 50% of available prey consumed and were thus not used in analyses. All five trials were in circular tanks during the 4-h dark experiments (Table 1). Results of all six experiment types differed significantly from expected frequencies if prey types were consumed in the same proportions as available (20% or 50% dead prey) (Table 1; Figures 1 and 2). Dead salmon were strongly selected during the light experiments; 20% dead prey were available, and 88.1% of consumed prey were dead (Table 1; Figure 2). When uneaten prey were counted during the 4-h periods of two light experiments (11 trials), it was found that most dead prey were eaten soon after being placed in the tanks; 22 of 27 dead prey consumed (81.5%) were ingested within 0.5 h after experiment initiation, and 26 of 27 dead prey (96.3%) were ingested within 2 h. During the same trials only 2 live prey were consumed, both within the first 0.5 h. Live prey were occasionally killed by northern squawfish but not ingested. Pharyngeal teeth marks on the sides of these individuals suggested that northern squawfish had attempted to swallow these prey tail-first and regurgitated them Regurgitated prey were classified as "consumed." In all experiments, 36 (11.4%) of the 315 consumed live prey were regurgitated. Only 3 (0.7%) of 441 consumed dead fish were regurgitated.

Table 1. Consumption of live and dead juvenile chinook salmon in six experiment types. Northern squawfish were offered either 20% or 50% dead prey in two experimental systems, 1400-L circular tanks (circ) or a 11,300-L raceway (RW). Three northern squawfish per tank were used for each circular tank trial, and 10 were used for each raceway trial. One set of trials was conducted in complete darkness (circ-dark; <0.01 lux), while an additional set of trials was in bright light only (circ-light; 215-270 lux). All other trials were in a natural photoperiod with both light and dark periods.

EXPERIMENT CONDITIONS				CONSUMED PREY			
percent dead	system	length (h)	no. of trials	total no.	percent dead	X^2	P
50	circ	24	18	332	61.8	18.3	<0.01
50	RW	3	3	132	78.8	43.7	co.01
20	circ	24	12	118	35.6	17.9	co.01
20	RW	3	3	36	36.1	5.8	<0.05
20	circ-dark	4	22*	79	31.2	6.7	<0.01
20	circ-light	4	22	59	88.1	171.2	<0.01

* = Twenty-seven circ-dark trials were conducted, but only 22 were used in analyses because during 5 trials >50% of the available prey were consumed.
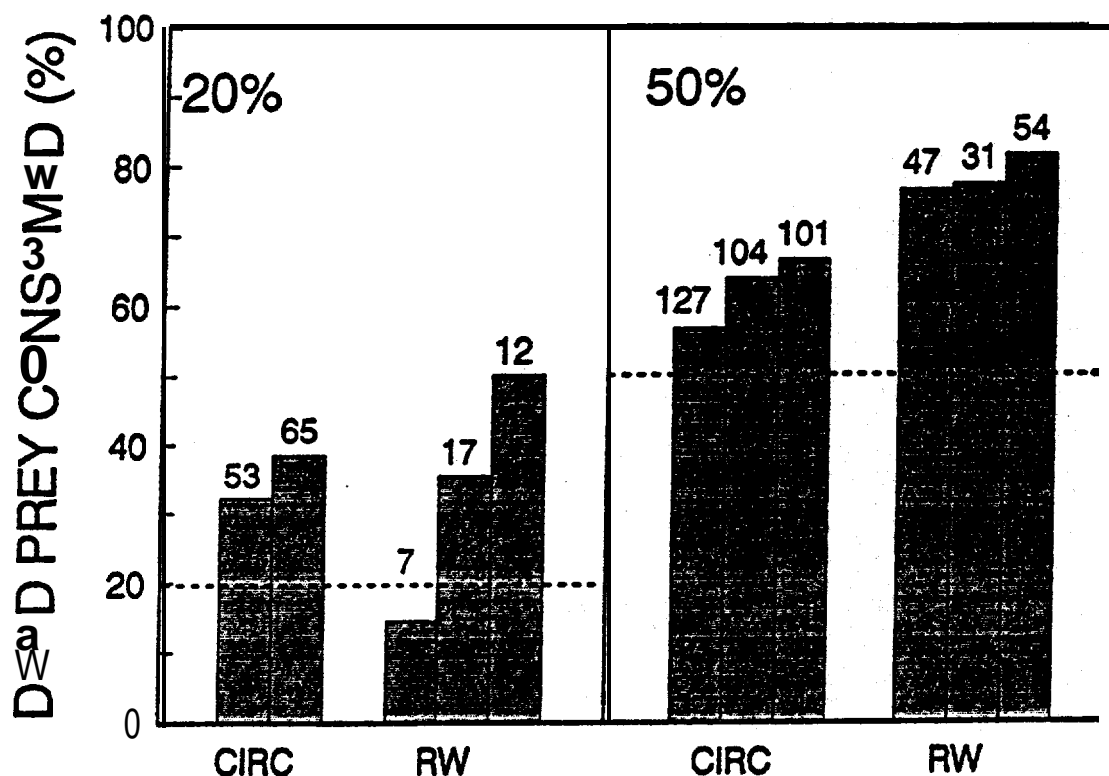
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DⱯD PREY CONS³MᵉD (%)

20%   50%

53 65   7 17 12   127 104 101   47 31 54

100
80
60
40
20
0

CIRC   RW   CIRC   RW

Figure 1.   Percentages of dead juvenile chinook salmon consumed by northern squawfish when offered both live and dead individuals.   Percentages of dead salmon initially available (20% or 50%) are indicated by horizontal dashed lines.   Each bar represents an individual trial conducted in a 11,300-L raceway (RW) for 3 h or combined results of six trials conducted in 1400-L circular tanks (circ) for 24 h. Numbers above bars are total numbers of live and dead consumed prey. Experiments are in order of increasing percentages of consumed dead prey.

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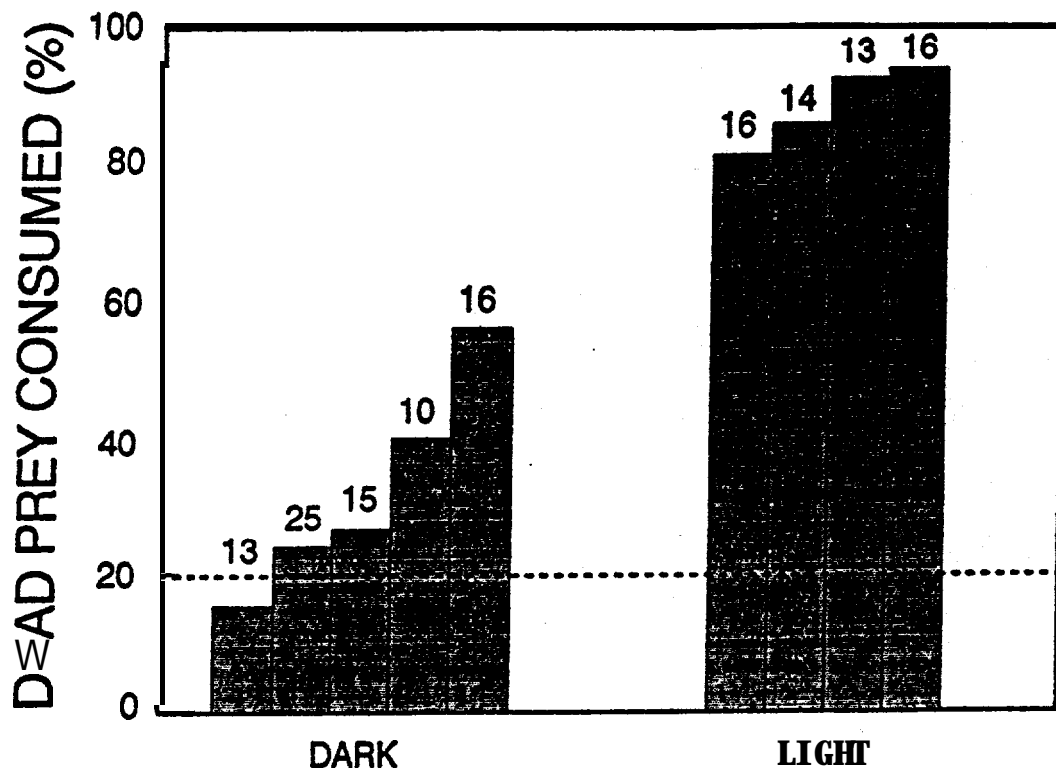
Figure 2.   Percentages of dead juvenile chinook salmon consumed
by northern squawfish when offered 80% live and 20% dead
individuals (indicated by horizontal dashed line) in either dark
(<0.01 lux) or light (215-270 lux) conditions.   Each bar
represents combined results of five or six trials conducted in
1400-L circular tanks for 4 h. Numbers above bars are total
numbers of live and dead consumed prey. Experiments are in order
of increasing percentages of consumed dead prey.

Discussion

Under-all experimental conditions, northern squawfish
consumed a significantly higher proportion of dead juvenile
chinook salmon than expected based on available ratios (Table 1).
Dead prey are not commonly reported to be selectively eaten by
fishes; moreover, for many fishes prey movement appears to be an
important feeding cue (Ware 1973; Howick and O'Brien 1983;
Irvine and Northcote 1983; Luczkovich 1988). Irvine and Northcote
(1983) found that underyearling rainbow trout _Oncorhynchus mykiss_
preferred live over dead prey and suggested that predators should
select moving prey to avoid ingesting nonnutritional (inorganic
or dead) material. Conversely, dead prey are more easily
captured than live prey, and nutritional value of newly killed
and live prey may be similar. Optimal foraging theory suggests
that predators should maximize their rate of energy intake by
preferentially selecting nonevasive prey if the energy content of
prey is equal (Ivlev 1961; Stephens and Krebs 1986). In a
location with significant numbers of new-ly killed prey, selection
of dead individuals might be advantageous.

Northern squawfish consumed a much higher percentage of
dead juvenile chinook salmon during experiments conducted in
bright light (88%) than during experiments in darkness (31%).
Light levels may affect predation by influencing both predator
activity and prey behavior (Cerri 1983). We have little
information on northern squawfish diel feeding behavior or
activity patterns. In the field, northern squawfish have been
reported to feed during both day and night periods, although
these feeding patterns were influenced by timing of prey
availability (Vigg et al. 1991). Prey behavior was very likely a
strong factor influencing our results. During darkness, live
prey are more at risk to predation due to decreased schooling
behavior and a reduction in reaction distance (Whitney 1969;
Emery 1973; Vinyard and O'Brien 1976; Cerri 1983), while dead
prey may possibly not be as easily detected due to their lack of
movement. In bright light, the ability of live juvenile salmon
to avoid northern squawfish might have resulted in preferential
consumption of dead salmon. The means by which northern
squawfish detect prey (vision, smell, water movements) are
unknown; this information would greatly aid in understanding the
results of _our_ experiments.

Northern squawfish captured but regurgitated 11% of all
consumed live chinook salmon. It is unknown if regurgitation
similarly occurs in the field; if so, this would bias estimates

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of predation mortality based on analysis of stomach contents. The direction of pharyngeal teeth-marks on regurgitated chinook salmon indicated that they were being held tail-first. Prey orientation when captured is unknown, but northern squawfish may prefer to swallow prey head.-first, as found for perch *Perca fluviatilis* (Hoogland et al. 1956), or prey may more easily escape if being held tail-first. Regurgitation could also be related to prey size.   Beyerle and Williams (1968) reported that northern pike *Esox lucius* eventually released larger prey they captured and unsuccessfully tried to swallow. Larger prey may be more difficult to manipulate and take longer to handle (Allan and Flecker 1988), resulting in prey escape or regurgitation.

In the field, the proportion of dead prey consumed by northern squawfish is unknown and can only be roughly estimated. We have shown that in the laboratory northern squawfish preferred dead over live juvenile salmon, both when prey types were equal, and when dead prey were present at a lower percentage (20%). However, the quantity of dead salmonids northern squawfish consume is dependent not only upon absolute proportions available, but also upon encounter rates between northern squawfish and live and dead salmonids; encounter rates are largely determined by fish movements and distribution patterns. In the laboratory, dead juvenile chinook salmon sank to the tank bottom and slowly drifted with water movements, whereas live individuals frequently schooled. Northern squawfish were often motionless near the tank bottom unless disturbed or feeding. In the field, fish activity and distribution patterns are difficult to determine.   Turbulence below dams probably keeps dead juvenile salmonids suspended and mixed with live salmonids for a period. Dead fish would eventually settle in areas with low water velocities such as back-eddies, while live salmonids move downriver.   Calm water areas are also preferred locations for northern squawfish (Faler et al. 1988), and thus northern squawfish in the field may frequently encounter dead juvenile salmonids.

Newly-killed juvenile salmonids in the Columbia River are more abundant immediately below dams [the boat-restricted-zones (BRZ)] than in other parts of the river system Rieman et al. (1991) estimated a combined spillway, turbine, and turbine bypass mortality of 4-10% at McNary Dam Consumption of juvenile salmonids by northern squawfish is also greatest at these sites. In John Day Reservoir during 1983-1986, approximately 26% of the 2.1 million juvenile salmon and steelhead lost seasonally to northern squawfish were consumed in the BRZ (Rieman et al. 1991).

Predation and dam passage mortality estimates may not be independent, however. Since we have shown that northern squawfish feed on dead prey, it is possible that a significant portion of the juvenile salmonids consumed by northern squawfish in the McNary Dam BRZ were already dead. Thus, the number of live juvenile salmonids consumed by northern squawfish may be less than previously assumed, suggesting that estimates of the overall impact of northern squawfish predation on salmonid populations should be adjusted. For example, if 20% of the juvenile salmonids ingested seasonally by northern squawfish in the McNary Dam BRZ were dead, then 0.11 million (2.1 million x 0.26 x 0.2) less live salmonids were killed by northern squawfish in this reservoir alone; a cumulative estimate of reduced predation impact in all reservoirs of the Columbia River would be much greater.

Acknowledgments

References

Allan, J.D., and A.S. Flecker. 1988. Prey preference in stoneflies: a comparative analysis of prey vulnerability. Oecologia 76:496-503.

Beamesderfer, R.D., and B.E. Rieman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society. 120: 439-447.

Beyerle, G.B., and J.E. Williams. 1968. Some observations of foodselectivity by northern pike in aquaria. Transactions of the American Fisheries Society 97: 28-31.

Cerri, R.D. 1983. The effect of light intensity on predator and prey behavior in cyprinid fish: factors that influence prey risk. Animal Behavior 31: 736-742.

Coutant, C. C., R. B. McLean, and D. L. DeAngelis. 1979. Influences of physical and chemical alterations on predator-prey interactions. Pages 57-68 in R. H. Stroud and H. Clepper, editors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington D. C.

Emery, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. Journal of the Fisheries Research Board of Canada 30: 761-774.

Faler, M. P., L. M. Miller, and K. I. Welke. 1988. Effects of variation in flow on distributions of northern squawfish in the Columbia River below McNary Dam North American Journal of Fisheries Management 8:30-35.

Hoogland, D. D. Morris, and N. Tinbergen. 1956. The spines of sticklebacks (Gasterosteus and Pyaosteus) as a means of defense against predators (Perca and Exox). Behavior 10:205-236.

Howick, G. L., and W. J. O'Brien. 1983. Piscivorous feeding behavior of largemouth bass: an experimental analysis. Transactions of the American Fisheries Society 112:508-516.

Irvine, J. R., and T. G. Northcote. 1983. Selection by young rainbow trout (Salmo gairdneri) in simulated stream environments for live and dead prey of different sizes. Canadian Journal of Fisheries and Aquatic Sciences 40:1745-1749.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University. Press, New Haven, Connecticut.

Lucchetti, G. L., and G. A. Gray. 1988. Prototype water reuse system The Progressive Fish-Culturist. 50:46-49. Luczkovich, J. J. 1988. The role of prey detection in the selection of prey by pinfish Laaodon rhomboides (Linnaeus). Journal of Experimental Marine Biology and Ecology 123:15-30.

Poe, T. P, H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating

juvenile salmonids in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society. 120: 405-420.

Raymond, H. L.   1968. Migration rates of yearling chinook salmon in relation to flows and impoundments in the Columbia and Snake Rivers.   Transactions of the American Fisheries Society 97:356-359.

Raymond, H. L.   1988. Effects -of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River Basin. North American Journal of Fisheries Management 8:1-24.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P..Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River.   Transactions of the American Fisheries Society. 120: 448-458.

Schoeneman, D. E., R. T. Pressey, and C. D. Junge. 1961. Mortalities of downstream migrant salmon at McNary Dam Transactions of the American Fishery Society 90:58-72.

Sims, C. W., J. G. Williams, D. A. Faurot, R. C. Johnsen, and D. A. Brege. 1981.   Migrational characteristics of juvenile salmon and steelhead in the Columbia River basin and related passage research at John Day Dam, Volumes I and II. Report to the U. S. Army Corps of Engineers. U. S. National Marine Fisheries Service.   Northwest and Alaska Fisheries Center, Seattle, Washington.

Stephens, D. W, and J. R. Krebs.   1986. Foraging Theory. Princeton University Press.   Princeton, New Jersey.

Temple, S. A. 1987.   Do predators always capture substandard individuals disproportionately from prey populations? Ecology 68:669-674.

Vigg, S. 1988. Functional response of northern squawfish predation to salmonid prey density in McNary tailrace, Columbia River.   Pages 174-210 in T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-

AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.

Vigg, S., and C. C. Burley. 1989. Temperature dependent maximum daily consumption of juvenile salmonids by northern squawfish (Ptychocheilus oregonensis) from the Columbia River. Report (contract DE-AI79-88BP92122) to Bonneville Power Administration, Portland, Oregon.

Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative preyfish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120: 421-438.

Vinyard, G. L., and W J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (Lepomis macrochirus). Journal of the Fisheries Research Board of Canada 33: 2845-2849.

Ware, D. M 1973. Risk of epibenthic prey to predation by rainbow trout (Salmo gairdneri). Journal of the Fisheries Research Board of Canada 30:787-797.

Whitney, R. R. 1969. Schooling of fishes relative to available light. Transactions of the American Fisheries Society. 98: 497-504.

Report 2

Northern squawfish predation on live and dead juvenile salmonids in the Bonneville Dam tailrace

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Abstract

Juvenile Pacific salmonids Oncorhynchus spp. that have been killed or injured during dam passage may be highly vulnerable or preferred prey of predators that aggregate below dams. Consequently, predation loss estimates based on dietary analyses may be too high. Field experiments were conducted in the Bonneville Dam tailrace (Columbia River) to compare predation rates by northern squawfish Ptychocheilus oreaonensis on live and dead juvenile salmonids. Known numbers of coded-wire tagged live and dead chinook salmon Q. tshawytscha were released into the tailrace on six nights, northern squawfish were collected after each release, and predator stomach contents were examined for prey tags. When 50% of salmon released were dead, northern squawfish consumed 60% dead salmon and large northern squawfish (>300 mm fork length) captured more dead salmon than small predators. When 10% of salmon released were dead, 22% of the tags in predator's guts were from dead salmon. These results corroborate laboratory studies and suggest that salmonid losses to northern squawfish should be re-evaluated.

Introduction

Estimated losses of juvenile Pacific salmonids Oncorhynchus spp. to predation by northern squawfish Ptychocheilus oreaonensis are high in the small (≈ 0.5 km^2) area just below McNary Dam on the Columbia River (Rieman et al. 1991). Estimates of predation mortality may be too high if the diet of northern squawfish includes salmon that have already been killed or injured during dam passage. Roughly 11% of the salmon that pass through turbines die, while 2% of all salmon going over the spillway are killed (Schoeneman et al. 1961). In laboratory

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predation experiments (Gadomski and Hall-Griswold 1992), northern squawfish preferred dead over live juvenile salmonids. The primary objective of this study was to examine, in field experiments in the Columbia River, northern squawfish feeding preferences for live versus dead juvenile salmonids.

Demonstration of selective predation requires measurement of the relative availability of different prey types to the predator, which is compared to the actual diet proportions of the predator (Ivlev 1961; Chesson 1978). Laboratory studies of fish optimal foraging often compare encounter rates with diet proportions (e.g., Werner and Hall 1974; Mittelbach 1981), whereas field studies of fish feeding usually compare some index of prey availability with diet data from predator gut contents (Ivlev 1961; Pearre 1982). Field measures of prey availability are often questionable, especially if predators and prey are highly mobile or prey have refugia (Zaret 1980). Some assumptions that must be made concern the relative abundance and distribution of prey and predators, actual encounter frequencies, and individual versus group behaviors.

An alternative technique for examining predator selection in the field is to control prey availability by releasing known numbers of prey, "recapture" marked prey in the guts of predators, and test for preference. Hargreaves (1988) used this technique in a field study to determine if natural fish predators were size selective when feeding on juvenile pink salmon O. gorbuscha. We used this technique to test northern squawfish selection on two prey groups - a control (live prey) and a treatment (dead prey). Known proportions of marked treatment and control groups were released, and tags were recovered later from predator guts.

Results reported here are preliminary, since some data collection (e.g., diets of predators) and analyses are continuing.

Methods

Experiments were conducted with two different release proportions: 50% live vs. 50% dead prey ("50:50 releases"), and, 10% dead vs. 90% live prey ("10:90 releases"). The 50:50 releases were designed to test the general "selective" behavior of northern squawfish when prey types were equally abundant, while the 10:90 releases approximated the live to dead ratios in a typical tailrace zone (Schoeneman et al. 1961). Four 50:50 release experiments and two 10:90 releases were conducted (Table 1). Experiments were done in 1990 and 1991 (Table 1); procedures were the same in both years, except where noted.

Prey were juvenile chinook salmon <u>Oncorhynchus tshawytschg</u> from the Little White Salmon National Fish Hatchery Complex. Juvenile salmon for the 1990 experiments were held in 1400-L, 1.5-m diameter circular tanks at the Columbia River Field Station (CRFS), whereas salmon for the 1991 experiments were held in hatchery raceways. - All tanks had flow-through well water at 7-8°C. Salmon were maintained with a commercial diet of 2.5 mm moist pellets.

Salmon were marked with binary-coded wire tags (Jefferts et al. 1963) and allowed at least 25 days for recovery before field release. Tag retention was high (≥95%) in all marked groups (7-8% of all fish in a group were tested), except salmon tagged for Expt. 2 in 1990, which had 60% and 72% tag retention. Percent tag retention was used in estimating the total number of marked fish released in a category.

In 1990, salmon were acclimated to river temperature before release by increasing water temperature 1°C per day over about a I0-day period. Because salmon used in 1991 were held in raceways, maintenance water temperature could not be gradually increased. In 1991, fish were acclimated to river temperature while being held in aerated, 845-Ltransportation tanks. Using flow-through heated water, temperature was gradually increased over an 10-h period immediately prior to release.

On the day of a release experiment, two uniquely-tagged groups of juvenile salmon were moved from the CRFS to Bonneville Dam in aerated 114-L containers (maximum 500 fish/container) or 845-Ltransport tanks (maximum 5000 fish/tank). One group of salmon was killed immediately before release with a backpack electroshocker (900 volts DC at 90 Hz for 20-30 s). Live and dead fish were released through a fish transportation hose (about 20 cm diameter), which emptied at the bottom of the bypass outlet below Bonneville Dam Powerhouse I (Figure 1). In 1990, alternating batches of live and dead salmon (about 500 fish per batch) were flushed through the transport hose with pumped river water; release of fish required about 20 minutes and rinse water was pumped through the release hose for at least 1 hr after each release. In 1991, live and dead fish were first mixed in one of the large transport tanks, and all fish were released together. Releases for all experiments began at approximately 2000 h during dusk light conditions.

Collection of northern squawfish began one hour after release of tagged juvenile salmonids and continued for about nine hours. The sampling period was limited so that tags ingested early in the evening would not be evacuated from the gut before a predator could be captured. Two 5.5-m electroshock boats were used to collect northern squawfish. Five areas ("Zones") of the Bonneville tailrace were selected for sampling, based upon prior studies and accessibility

Table 1. - Experiment dates, total number of salmon released, dead-live ratio, and mean lengths of released juvenile salmon.

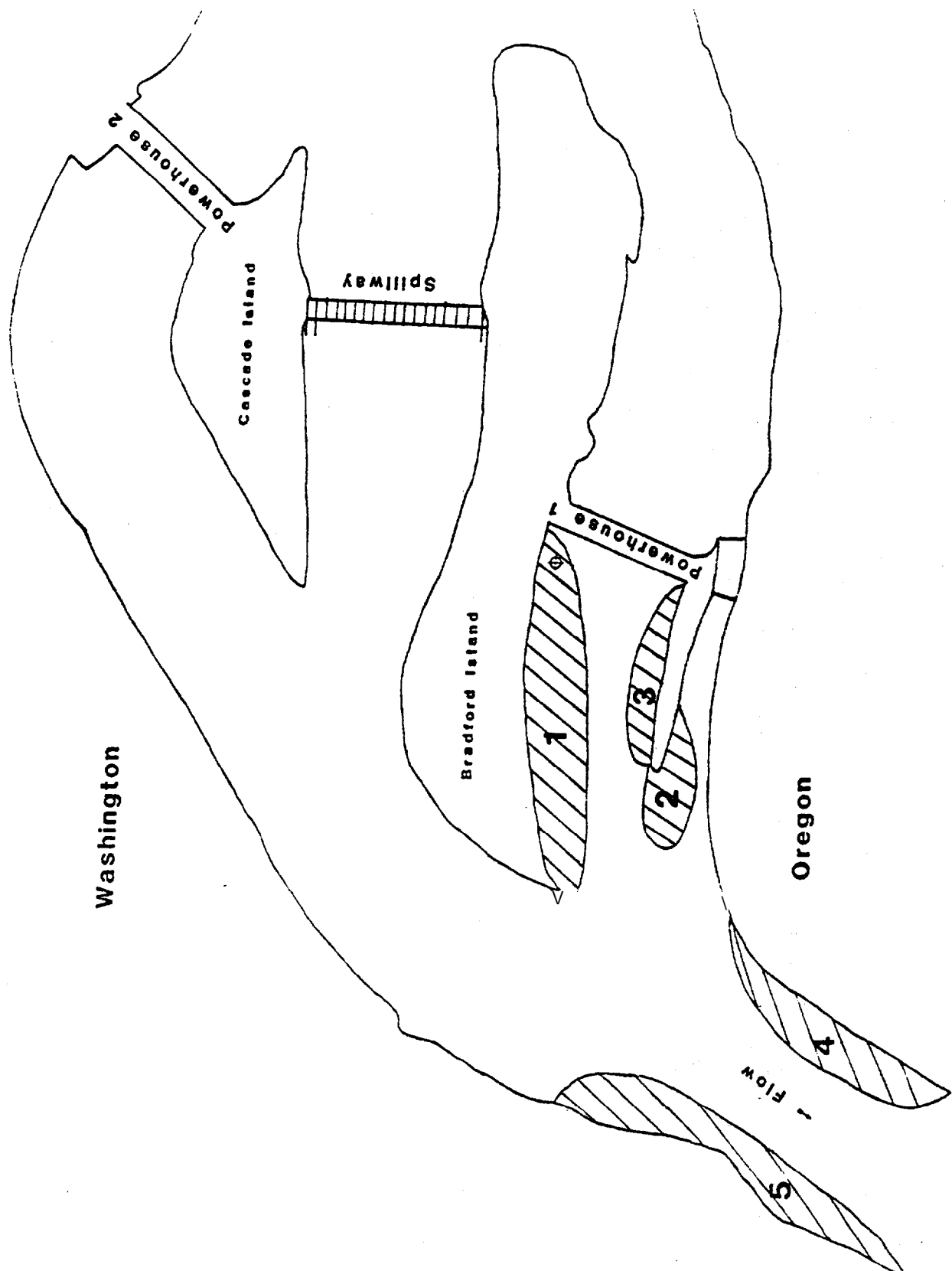| Expt.	Release Date			Total # Salmon Released	Dead:Live Ratio	Mean Fork Length - mm (SD)	
						Live	Dead
1	Aug.	27,	1990	5,095	52:48	93 (7)	90 (7)
2	Aug.	28,	1990	3,056	57:43	92 (7)	94 (7)
3	Aug.	27,	1991	10,000	10:90	93 (7)	93 (9)
4	Aug.	29,	1991	10,000	50: 50	90 (8)	92 (10)
5	Sep.	3,	1991	10,000	50:50	90 (8)	92 (10)
6	Sep.	5,	1991	10,000	10:90	93 (9)	93 (7)

Figure 1. - Location of northern squawfish sample transects in the Bonneville Dam tailrace. Point of release of tagged salmon is shown downstream from Powerhouse 1 (Θ).

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(Figure 1); Zones 2 and 3 were combined during 1991 studies. Sampling effort was primarily along the south shore of Bradford Island (Zone 1), immediately downstream of the release site. Turbine units 9 and 10 of Powerhouse I were shut down by the Army Corps of Engineers to facilitate boat access to Zone 1.

All northern squawfish that surfaced from electroshocking were netted, except those lost to swift current. Northern squawfish were killed onboard by a lethal dose of tricaine and returned to a shore processing site within about 45 minutes of capture. All northern squawfish were measured for fork length (FL, nearest mm) and total weight (nearest 10 g), and sexed if possible. Guts of al.1 northern squawfish greater than 250 mm FL were removed, placed in plastic bags, and preserved on ice; guts of smaller individuals were opened and collected if they contained recently-ingested salmon.

In the laboratory, frozen guts were thawed and processed using a digestive enzyme technique (Petersen et al. 1990). Enzyme solution was prepared using lukewarm tapwater, 2% (by weight) strength pancreatin, and 1% sodium sulfide. The solution was poured into plastic bags containing guts. Bags were sealed and placed in a 40°C dessicating oven for 24 hrs. After all flesh was digested, contents of a bag were agitated and CWTs accumulated at the bottom of the bag because of their high density. Tags were collected and samples were additionally checked for CWTs using an electronic tag detector. Remaining contents were rinsed through a 425 micron sieve with tapwater and diagnostic bones (primarily cleithra, dentaries, and opercles; Hansel et al. 1988) were removed. Diagnostic bones were identified and paired to enumerate prey fish consumed. Binary codes on CWTs were read using a compound microscope.

Statistical Methods.-Two analytical approaches were used to test hypotheses about selection of live and dead prey by northern squawfish.

For the first analysis, we considered the overall effect of the local northern squawfish population on salmon release groups by using the daily numbers of all live and dead salmon consumed as replicates. Observed and expected frequencies of live and dead salmon captured were compared using the chi-square statistic (Sokal and Rohlf 1981). Expected frequencies of live and dead salmon consumed for a day were based on the number of marked salmon released in each prey category. The power $(1-\beta)$ of chi-square tests was computed by formulas in Sokal and Rohlf (1981) and Elrod and Franks (1990).

For the second analysis, we were primarily concerned with the feeding behavior of individual northern squawfish (replicates); the dependent variable was the number of tags from live and dead salmon found in each predator gut. Independent variables in the analysis

were northern squawfish size (FL), location of capture (Zone), experiment number (day), and the elapsed time (h) following release that the predator was caught. Analysis of covariance (ANCOVA) was used to test for differences in the proportion of dead prey, which was . arcsin transformed using the method of Snedecor and Cochran (1980, p. 290). Because of low predator catches and negligible tag returns in Zones 2, 3, and 4 on the Oregon shoreline (Table 2), we combined these three zones during ANCOVA analyses. The times of predator capture were grouped into 2-h intervals for ANCOVA analyses.

Both types of analyses were done for 50:50 and 10:90 releases.. The 50:50 release experiments in 1990 and 1991 were considered replicates for chi-square analysis, although release proportions were slightly different from 50:50 live vs. dead on both 1991 dates(Table 1). In Expt. 2 (August 28, 1990) the release proportion was 43% live to 57% dead because of poor tag retention in two fish groups. Relatively few tags were recovered during Expt. 2 (30 tags), compared to the other 50:50 replicates (75, 106, and 119 tags, Table 3).

Table 2. - Total catch of northern squawfish (number with CWTs in gut) by fishing zone during each release experiment. Catches from Zones 2 and 3 were not separated during 1991 experiments (Expts. 3-6). See Table 1 for release dates.

Expt.	Zone					Total
	1	2	3	4	5	
1	235 (24)	48 (0)	36 (2)	23 (3)	56 (4)	390
2	113 (19)	28 (0)	6 (0)	43 (0)	63 (0)	253
3	155 (75)	36 (1)		61 (6)	98 (5)	350
4	47 (20)	24 (0)		11 (0)	51 (7)	133
5	53 (27)	11 (0)		22 (0)	44 (5)	130
6	38 (17)	27 (0)		17 (0)	45 (1)	127
TOTAL	641 (182)	216 (3)		177 (9)	357 (22)	1391

Table 3. - Numbers of expected and observed tags recovered from northern squawfish guts during six release experiments. Expected tag numbers are based on release proportions of live vs. dead salmon (see Table 1). P is the probability that observed and expected are significantly different (* P<.05; *** P<.001; NS Not Significant).

Expt.	Tags from LIVE		Tags from DEAD		Chi-Square	df	P
	Observed	Expected	Observed	Expected			
50:50 Releases							
1	27	36.2	48	38.8	4.5	1	*
2	13	12.9	17	17.1	0.0	1	NS
4	52	53.0	54	53.0	0.0	1	NS
5	33	59.5	86	59.5	23.6	1	***
Total	125	156.0'	187	156.0'	28.1[2]	4	***
Pooled'					13.1	1	***
Heterogeneity					15.0	3	***
10:90 Releases							
3	179	212.4	57	23.6	39.3	1	***
6	31	28.8	1	3.2	2.2	1	NS
Total	210	241.2	58	26.8	41.5[2]	2	***
Pooled					31.4	1	***
Heterogeneity					10.1	1	***

'Assumed a 50:50 prey ratio for all experiments in this calculation.

[2]Based upon summation of chi-square values for separate experiments.

Results

Northern Sauawfish Catch

A total of 1391 northern squawfish were captured during the six nights of sampling (Table 2). Nightly catches ranged from 127 to 398 (Table 2). Most northern squawfish (46.1%) were caught in Zone 1 near the Prey release point; catches from the Oregon shore (Zones 2-4, 28.2%) and the Washington shoreline (Zone 5, 25.7%) were similar.

Of 1391 northern squawfish collected, 216 fish (15.5%) contained at least one CWT. The average tag return rate for the six experiments was:

5.7 CWTs recovered • 1000 CWTs released-' • 100 predators captured-'
(SD = 2.7, N=6).

Northern Sauawfish Diet and Alternative Prev

River conditions and passage rates of juvenile salmonids were similar among all six nights (Table 4). River flow and temperature were slightly higher during 1990 experiments, compared to 1991. Passage of juvenile American shad _Alosa sapidissim_ was much higher during 1990 releases than during the 1991 experiments (Table 4). In late August 1990, about 5000 juvenile shad passed Bonneville Dam Powerhouse 1 daily, whereas very few juvenile shad were passing during the same period in 1991 (data from Rick Martinson, National Marine Fisheries Service, Bonneville Dam Smolt Monitoring Project).

Complete diet data for northern squawfish are not available at this time. During 1990, the diet of northern squawfish consisted of about 20% juvenile salmonids, 79% juvenile American shad, and 1% other fish. We expect northern squawfish diets from 1991 to contain a smaller percentage of juvenile American shad because of the lower numbers of them migrating through the river (Table 4). Less than 1% of northern squawfish regurgitated their stomach contents after collection.

Live vs. Dead Prev Selection

Juvenile salmon length was not significantly different (P<.05) among the six release lots (Table 1). During four nights when salmon releases were approximately 50% live and 50% dead, northern squawfish guts contained 187 (60%) tags from dead salmon

Table 4. - River flow, temperature, and relative abundance of migrating salmonids and American shad at Bonneville Dam Powerhouse No. 1 during six release experiments. The Passage Index for salmonids is the total number of sampled salmon and steelhead that were collected at the powerhouse during an 8-h period (Fish Passage Center, Weekly Reports).

| Expt. | River Flow (kcfs) | Water Temperature (°C) | In-River Salmonids | | Juvenile Am Shad Passage (count) |
			Passage Index	Mean Length of sub-yearling chinook salmon[1] (mm FL)	
1	159.0	21.1	770	119	5794
2	155.5	21.1	890		4715
3	140.1	17	857	110	145
4	118.0	18	558	123	115
5	119.1	18	1,035	123	114
6	111.3	17	508	122	131

[1]During 1991 releases (Expts. 3-6), about 5% of fish passing Bonneville Powerhouse No. 1 were yearling chinook salmon (mean length 144 mm). No other salmonid species were recorded at Bonneville Dam during 1990 or 1991 release experiments.

chi-square statistic for individual days (Table 3). Proportions were significantly different from the expected proportions on only two of four days, however, suggesting between-day heterogeneity.

For the two release dates with 10% dead and 90% live salmon, the results of the overall frequency analysis was similar to the 50:50 results (Table 3). Total and pooled data (22% dead prey captured:78% live prey captured) were highly different from the expected 10:90 release ratio, but between-day heterogeneity was also significant. On one day (Expt. 6), only 32 tags were recovered from northern squawfish guts and the expected and observed frequencies were not different (Table 3); for the other release day (Expt. 3), however, 268 tags were recovered and significantly more tags were from dead salmon than were expected (Table 3).

The power (1-p) of testing a prey selection hypothesis with chi-square depends upon sample size, the testing level (a), and the percent change from initial release proportions that an investigator wishes to detect (Sokal and Rohlf 1981; Elrod and Franks 1990). The percent change from expectation in the 50:50 release experiments was about 20% (0.50 dead salmon released to 0.60 dead salmon recovered). Daily sample sizes ranged from 30 to 119 tags recovered (Table 3). The power of daily releases to detect a 20% change was low $(1-\beta<0.6; \alpha=.05)$; however, the power of the test was very high $(1-\beta>0.95; \alpha=.05)$ when daily tag frequencies were pooled. For the 10:90 releases (both days pooled), the power of the chi-square test to detect the observed percent change was also very high $(1-\beta>0.95; \alpha=.05)$.

In the second set of analyses (ANCOVA), the size of the predator and the time of capture had significant $(P<.05)$ effects on the mean proportion of dead tags in individual northern squawfish guts during 50:50 releases (Table 5). For 10:90 releases, no significant treatment effects were found (Table 5). Capture time and size of predator were not correlated during either set of release experiments $(P>.30)$ suggesting these factors were independent.

The proportion of tags from dead salmon found in northern squawfish guts increased slightly with time after release (Figure 2). During the first 2 hours after salmon were released in 50:50 experiments, the proportion of dead prey in northern squawfish guts was less than expected (Figure 2), but this proportion increased for predators captured later in the night. In the 10:90 releases, the pattern for the mean proportion dead was similar to that in the 50:50 experiments (Figure 2), although the 10:90 means were not statistically different from one another (Table 5).

In both 50:50 and 10:90 releases, the proportion of dead salmon eaten by northern squawfish increased with increasing predator size, to at least 375 mm FL (Figure 3). The largest (> 400 mm FL) northern

Table 5. - ANCOVA for the effects of predator length, hours following prey release of predator capture, capture zone, and experiment (Day) upon the proportion of CWTs from dead salmon in northern squawfish guts.

50:50 Releases

Source of Variation	SS	d.f.	MS	F	P
Model	2.54	9	0.28	2.43	.02
Covariate					
Predator Length	0.60	1	0.60	5.19	.02
Main Effects					
Time of Collection	1.08	3	0.36	3.09	.03
Day	0.41	3	0.14	1.95	.32
Zone	0.45	2	0.23	1.95	.15
Residual	11.61	100	0.12		
Total (Corrected)	14.15	109			

10:90 Releases

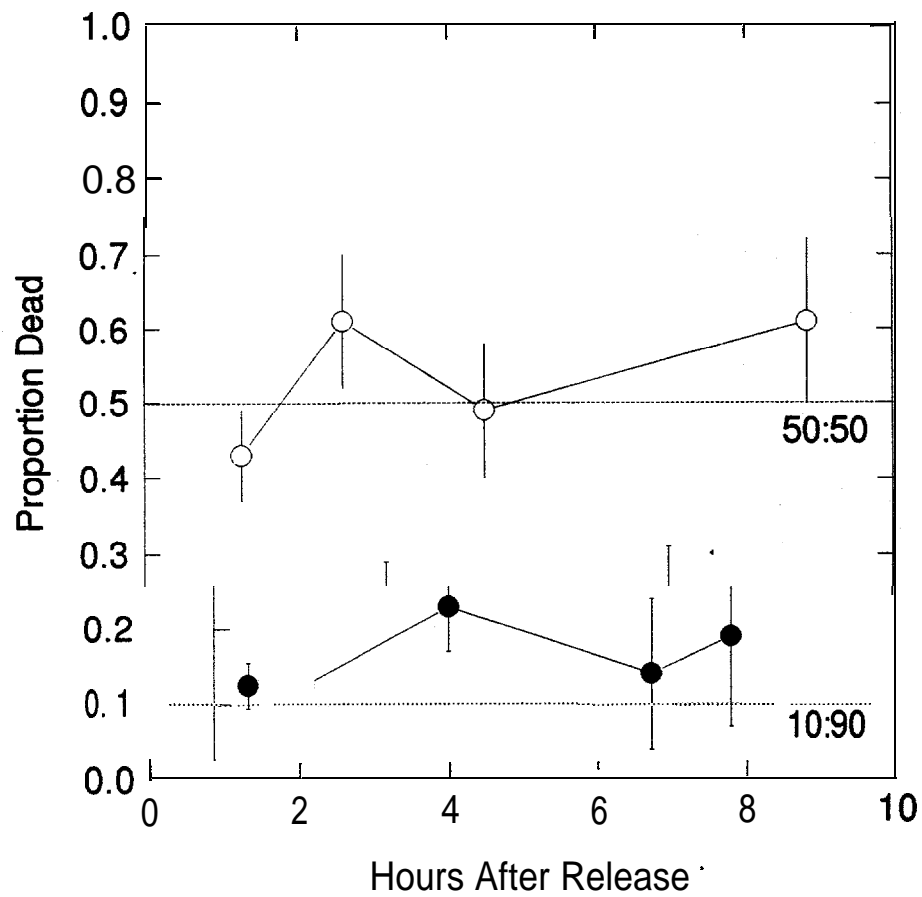| Source of Variation	SS	d.f.	MS	F	P
Model	0.22	7	0.03	0.66	.71
Covariate					
Predator Length	0.00	1	0.00	0.07	.79
Main Effects					
Time of Collection	0.08	3	0.03	0.51	.67
Day	0.14	1	0.14	2.83	.10
Zone	0.01	2	0.00	0.01	.93
Residual	4.61	94	0.05		
Total (Corrected)	4.83	101			

Figure 2. - Mean (SE) proportion of tags from dead salmon recovered from northern squawfish guts collected at various times. Results for 50:50 and 10:90 release experiments are shown.
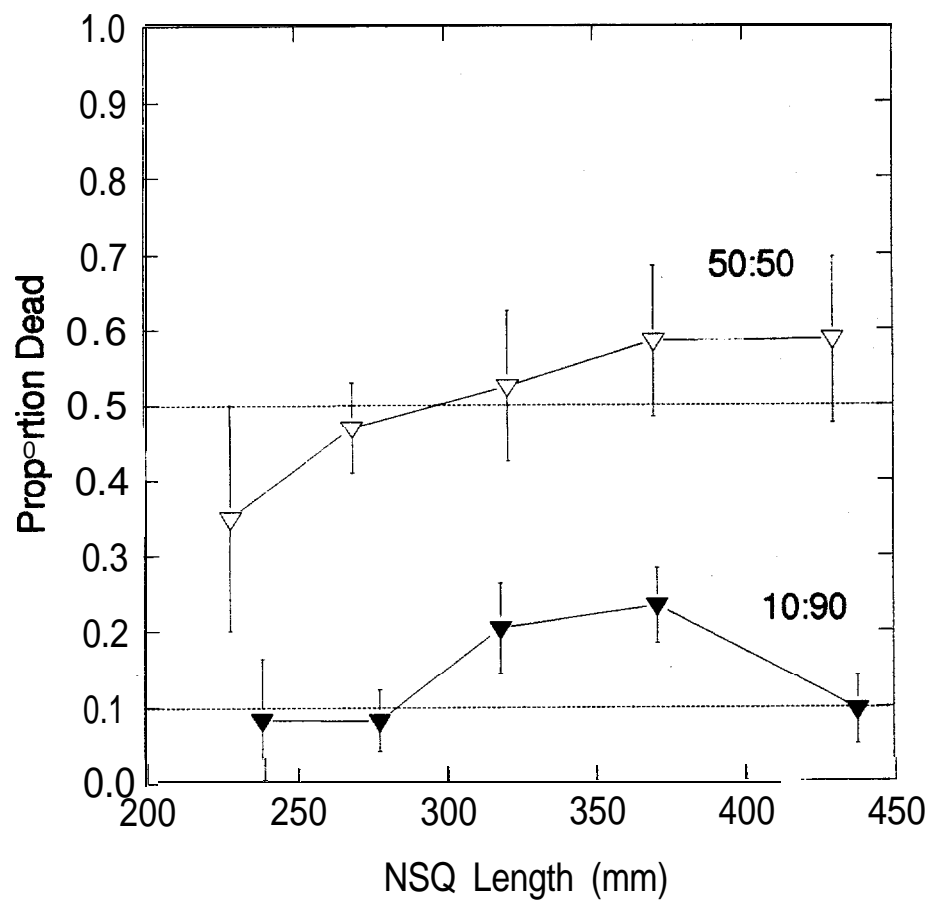
Figure 3. - Mean (SE) proportion of ail tags in northern squawfish (NSQ) guts that were from dead salmon. Results for 50:50 and 10:90 release experiments are shown.

squawfish collected during 10:90 releases had a lower proportion of dead salmon in their guts compared to the largest predators sampled during the 50:50 releases (Figure 3). The number of dead salmon captured was significantly related to predator size in the 50:50 releases, but not in the 10:90 releases (Table 5).

The feeding activity, or rate, of northern squawfish increased with predator size during 50:50 releases, but size had no effect during the 10:90 releases (Figure 4). The mean feeding rate of northern squawfish was not significantly different between 50:50 and 10:90 releases (&-test, P=0.15).

Discussion

The primary goal of this study was to test a specific hypothesis about predation-caused mortality of juvenile salmon when dead salmon are also available. A secondary goal was to develop and refine a field method for testing predation hypotheses.

Feasibility of methods

CWTs have been used extensively on juvenile salmonids in the Columbia River Basin (e.g., Ebel et al. 1973; Wahle et al. 1981). Prey selection studies require that care be taken to determine the relative proportions of fish in different groups at the time of release so the expected proportions of each group consumed can be calculated. In our studies, one logistical problem was poor tag retention in two groups of tagged salmon. Salmon examined from these groups indicated that tag loss was likely caused by improper adjustment of the tagging machine, causing some tags to be shed through the roof of the fish's mouth. CWT loss is usually less than 5% (Opdycke and Zajac 1981; Eames and Hino 1983); however, proper tag placement in the head of small fish is necessary for good retention (Ostergaard 1982).

Using electricity to kill salmon at the release site was efficient, rapid, and avoided potential problems that might be associated with chemical poisons (e.g., predator avoidance). Electroshocking has proven to be an effective method for collecting adult northern squawfish (Poe and Rieman 1988). Northern squawfish generally occur along shorelines in littoral and sub-littoral habitats (Faler et al. 1988; USFWS unpublished data), where electrofishing is most effective. Our sampling methods and design would be less effective for collecting northern squawfish in river depths greater than 5-6 m
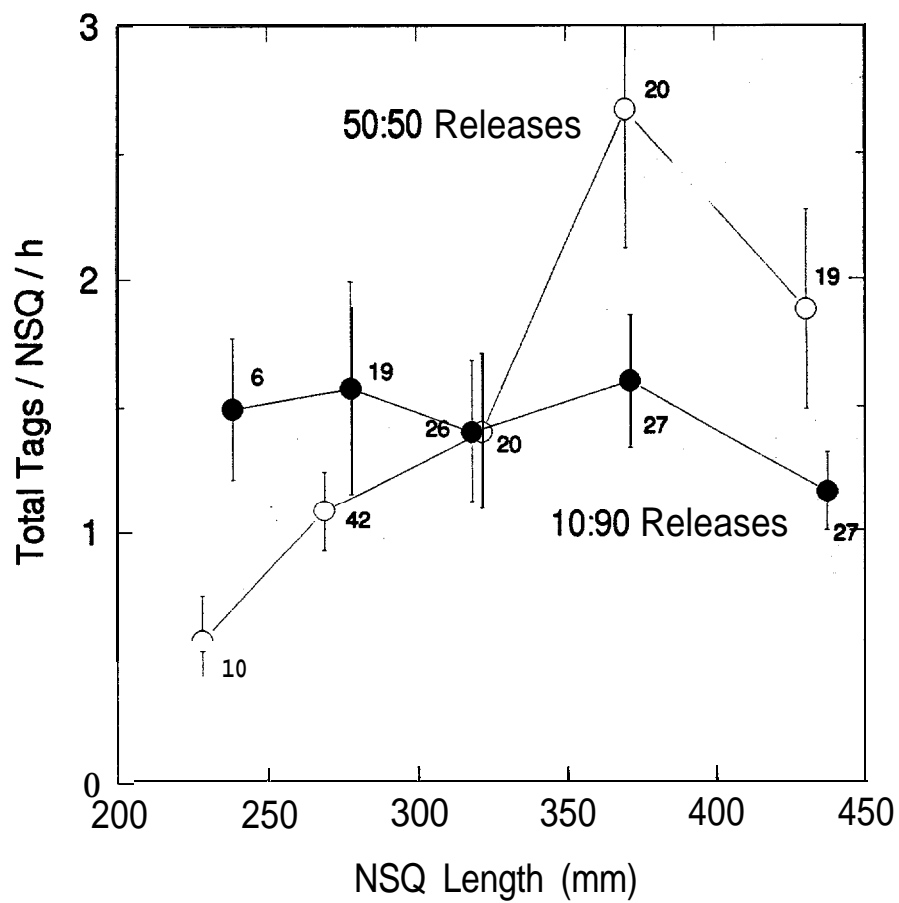
Figure 4. - Mean (SE) number of tagged salmon captured per hour by northern squawfish (NSQ) of various lengths. Results of 50:50 and 10:90 releases are shown. Numbers beside symbols are sample size.

Live vs. Dead Prey Selection

Our results corroborate laboratory studies of northern squawfish feeding behavior on live and dead salmon (Gadomski and Hall-Griswold, 1992). Gadomski and Hall-Griswold found that relatively large northern squawfish (mean FL of 433 mm, SD=36; n=70) selected dead juvenile salmon more often than expected (small northern squawfish were not used in their experiments). When 50% of available salmon were live and 50% were dead in laboratory experiments, 67% of all salmon eaten by northern squawfish were from the dead group (Gadomski and Hall-Griswold, 1992), similar to our field results ($\approx$60% dead prey selected; Figure 3). Also similar to our results, Gadomski and Hall-Griswold found that dead salmon were consumed at a higher than expected rate in the laboratory when smaller proportions (20%) of all offered salmon were dead.

Comparing 50:50 and 10:90 field release results suggests that the largest predators may be stimulated to feed more rapidly when a high proportion of dead prey are available. In the 50:50 field experiments, large northern squawfish feeding rate was higher than observed in smaller fish, and the proportion of dead prey in the diet of the largest predators was also higher (Figures 3 and 4). This pattern was not apparent in the 10:90 releases. These results suggest some feeding interaction between large and small predators when many dead salmon were present.

Heterogeneity in live and dead capture proportions between replicate release dates (Table 3) may have been partly caused by small sample sizes on some nights. Replicate chi-square values were highly correlated with the number of tags recovered ($r=0.90$, $P<.02$), suggesting a strong sample size effect. The capture proportions of live and dead salmon did not differ from expectation on three of six individual nights; however, two of the three nights with non-significant results also had the smallest numbers of recovered tags ($N=30$, $N=32$). In Experiment 4, a moderate number of tags were recovered ($N=106$), but the proportion of live to dead prey was almost exactly the same as the release proportion (Table 3).

Day-to-day heterogeneity may also have been influenced by the scheduling of experiments and prior sampling in the Bonneville Dam tailrace. All three experiments where capture proportions were not significantly different from release proportions were conducted on nights when another experiment had been performed within 1-2 days (Tables 1 and 3); experiments with significant results were conducted following at least four nights with no electroshock or boat activity in the tailrace. Electroshock sampling may have disrupted the feeding behavior of northern squawfish, or several days might be necessary for large predators to return to the tailrace following shocking.

Prev Availabilitv

Tests of food selection by a predator usually require quantifying the availability of different food types with various indicies (reviewed by Cock 1978; Pearre 1982). An important assumption for testing "selection" hypotheses is that the availability of the different prey groups is known and remain constant during the course of the experiment (Hargreaves 1988). Our experiments were designed so initial prey availability would be known, but we did not attempt to estimate availability during the predation period. Prey availability likely changed over time in a complex, and perhaps rapid, manner.

In a natural situation, prey availability may be affected by many processes. The tailrace of a dam is a turbulent area, which should have ensured mixing of our two prey groups. Also, separation of live and dead salmon in the tailrace experiments was limited by collecting northern squawfish over a fairly short time following prey release, decreasing the time available for separation. Observations of live and dead salmon in a flowing-water raceway at our laboratory showed that dead salmon could be suspended by only moderate turbulence; live and dead prey remained well mixed until the dead fish drifted to the downstream end of the tank.

Another reason for not monitoring prey availability was the specific hypothesis we were testing. We were primarily interested in quantifying the realized selection upon the prey groups, rather than measuring the selection or capture success of predators given equal chances at prey types. If water currents or salmon behavior separate live and dead prey in the tailrace under normal conditions, availability may vary for different prey groups, and be a cause of the differential predation. The null hypothesis tested by these experiments was that the in-river capture rates on live and dead salmon were proportional to the release numbers - not specifically that individual predators behaviorally select live or dead prey.

The higher proportion of dead salmon consumed by large northern squawfish in the Bonneville Dam tailrace might be a result of the higher availability of dead prey to large, competitively superior northern squawfish. Water velocity and turbulence decrease downriver from the dam, perhaps causing dead salmon to collect behind boulders and in other calm water areas. One northern squawfish that had 14 CWTs from dead salmon was collected from Zone 5, about 1 km downriver from the release site. Large predators may occupy feeding stations in the tailrace where dead prey tend to collect because of eddies or currents, while smaller predators are forced to forage in faster, more turbulent water. The capture success (on both dead and live prey) for predators foraging in calm water might be higher than for predators in high-flow environments, who must contend with both turbulence and prey escape responses.

References

Chesson, J. 1978. Measuring preference in selective predation. Ecology 59:211-215.

Cock, M 3. W 1978. The assessment of preference. Journal of Animal Ecology 47:805-816.

Eames, M J. and M K. Hino. 1983. An evaluation of four tags suitable for marking juvenile chinook salmon. Transactions of the American Fisheries Society 112:464-468.

Ebel, W J., D. L. Park, and R. C. Johnsen. 1973. Effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. Fishery Bulletin, U.S. 71:549-563.

Elrod, 3. H. and Franks, A. 1990. Sample size requirements and analysis of tag recoveries for paired releases of lake trout. North American Journal of Fisheries Management 10:196-201.

Faler, M P., L. M Miller, and K. I Welke. 1988. Effects of variation in flow on distribution of northern squawfish in the Columbia River belwo McNary Dam North American Journal of Fisheries Management 8:30-35.

Gadomski, D. M and J. A. Hall-Griswold. In Review. Predation by northern squawfish on live versus dead juvenile salmonids. Transactions of the American Fisheries Society.

Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transactions of the American Fisheries Society 117:55-62.

Hargreaves, N. B. 1988. A field method for determining prey preference of predators. Fishery Bulletin, U.S. 86:763-771.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven.

Jefferts, K. B., P. K. Bergman, and H. F. Fiscus. 1963. A coded wire identification system for macro-organisms. Nature (London) 198:460-462.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study

of optimal diet and habitat use by bluegills. Ecology 62:1370-1386.

Opdycke, 3. D. and D. P. Zajac. 1981. Evaluation of half-length binary-coded wire tag application in juvenile chum salmon. Progressive Fish-Culturist 43:48.

Ostergaard, D. E. 1982. Retention of coded wire tags in lake trout. Progressive Fish-Culturist 44:162.

Pearre, S. Jr. 1982. Estimating prey preferences by predators: uses of various indicies and a proposal of another based on X^2. Canadian Journal of Fisheries and Aquatic Science 39:914-923.

Petersen, 3. H., M G. Mesa, 3. Hall-Griswold, W C. Schrader, G. W Short, and T. P. Poe. 1990. Magnitude and dynamics of predation on juvenile salmonids in Columbia and Snake River reservoirs. Annual Report of Research, 1989-1990. Bonneville Power Administration, Portland, Oregon.

Poe, T. P. and B. E. Riemann. 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir. Final Report, 1983-86. Bonneville Power Administration, Portland, Oregon.

Riemann, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:448-458.

Schoeneman, D. E., R. T. Pressey, and C. O. Junge, Jr. 1961. Mortalities of downstream migrant salmon at McNary Dam Transactions of the American Fisheries Society 90:58-72.

Snedecor, G. W and W. G. Cochran. 1980. Statistical methods, Seventh edition. Iowa State University Press, Ames, Iowa.

Sokal, R. R. and F. 3. Rohlf. 1981. Biometry, 2nd edition. Freeman, New York.

Wahle, R. J., E. Chaney, and R. E. Pearson. 1981. Areal distribution of marked Columbia River Basin spring chinook salmon recovered in fisheries and at parent hatcheries. Marine Fisheries Review 43:1-9.

Werner, E. E. and D. J. Hall. 1974. Optimal foraging and the size

selection of prey by the bluegill sunfish (_Lepomis macrochirus_).
Ecology 55:1042-1052.

Zaret, T. M   1980.   Predation and freshwater communities.   Yale
University Press, New Haven.

Report 3

**Effects of Experimental Descaling on Juvenile Salmonid
Vulnerability to Northern Squawfish Predation**

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Abstract

The. passage of juvenile salmonids through dams often results in
damage to the skin, scale, and slime complex. We conducted
laboratory experiments to determine if salmonids descaled on 10% or
20% of their total body area are more vulnerable to predation by
northern squawfish _Ptychocheilus oreaonensis,_ When offered equal
numbers of control and descaled juvenile chinook salmon _Oncorhynchus
tshawtschg,_ northern squawfish did not consume significantly
($P<0.05$) more of either prey type; at the 10% and 20% descaling
levels, 48-51% and 49-60% of consumed prey were descaled,
respectively. Our results indicate that descaling at low levels does
not cause increased vulnerability of juvenile salmonids to
predation.

Introduction

Many fishes passing through dam turbines, spillways, and
bypasses lose scales through abrasion (Kostecki et al. 1987; Koski
et al. 1990). The percentage of juvenile salmonids that are
descaled varies widely depending on location, season, year and
species (Koski et al. 1990). Damage to the skin, scale, and slime
complex of a fish may cause osmotic dysfunction or even death (Van
Oosten 1957; Black and Tredwell 1967; Bouck and Smith 1979; Kostecki
1987). Descaled fish may also be more susceptable to disease and
predation, although these possibilities have not been studied.
'It has been demonstrated that weaker prey may be captured in
higher than expected proportions by predators (Temple 1987), due
either to predator selection or to increased prey vulnerability. We
were specifically interested in determining if descaled juvenile
salmonids are preyed upon more heavily than healthy salmonids by the

northern squawfish <u>Ptychocheilus</u> <u>oreaonenesis</u>. The northern squawfish is a dominant predator of juvenile salmonids in the Columbia River (Rieman et al. 1991). Much of this predation occurs just below dams, where many salmonids may have recently been descaled due to dam passage. It is possible that northern squawfish are preferentially feeding on these individuals, and thus mortality of healthy salmonids due to predation may be less than previously estimated.

We tested northern squawfish predation on juvenile salmon that had been descaled on either 10% or 20% of their total body area, excluding head and fins. These levels were chosen based on criteria developed by the National Marine Fisheries Service Fish Transportation Oversight Team, a group that monitors juvenile salmonid out-migration at Snake and Columbia river dams. This criteria states that a fish is "descaled" if cumulative scale loss equals or exceeds 20% on one side of the body (Koski et al. 1990; Gessel et al. 1991).

Methods

Northern squawfish (449 mm fork length, FL; SD 39 mm, n = 78) were collected from the Columbia River by boat electroshocking. Fish were held in 1400-L indoor circular tanks (1.5 m diameter, 0.8 m deep) for an acclimation period of at least two weeks. All tanks were part of a recirculating water system (Lucchetti and Gray 1988) that provided a constant flow of 20 l/min to each tank. Water temperature was maintained at 15-17°C. Timer controlled fluorescent and incandescent lighting simulated a natural photoperiod: day (0700-2000), 215-270 lux; dusk (0600-0700 and 2000-2100), 1-2 lux; and night (2100-0600), <0.01 lux. Northern squawfish were fed a maintenance diet of live juvenile coho salmon <u>Oncorhynchus</u> <u>kisutch</u> (103.8 mm FL; SD 7.2 mm, n = 50) during acclimation and between experiments. Juvenile chinook salmon O. <u>tshawytscha</u> (96.7 mm FL; SD 8.9 mm, n = 584) were used as prey for experiments. Coho and chinook salmon were obtained from the Little White Salmon National Fish Hatchery Complex. All salmonids were maintained at densities of ≤ 7 kg/m in outdoor circular tanks (1.5 m diameter, 0.8 m deep) supplied with 7 ± 1°C well water. Juvenile salmonids were fed a maintenance diet of 2.5 mm commercial moist pellets. One week prior to an experiment chinook salmon were transferred to an indoor tank and acclimated to experimental temperatures.

We assessed northern squawfish predation on juvenile salmonids descaled on 10% or 20% of their total body area. Treatment fish were anesthetized with 60 mg/l tricaine methanesulfonate (MS-222) and a

rectangular patch of scales along the side was scraped off using a dull spatula. This patch was positioned dorsally to avoid the belly area, and extended from below the dorsal fin to the caudal region, including the lateral line. To achieve a total body descaling of 10%, scales were removed on 20% of one side of a juvenile salmon. For the higher descaling level, 20% of both sides were descaled. We used salmon with less than a 3% natural scale loss to maintain uniform descaling levels. Time for descaling an individual fish averaged 20 s.   To assure that treatment fish received a descaling patch that was the correct percentage of their body area, we measured descaled patch size (width X length) and fork lengths of 59 juvenile chinook salmon. We then determined the relation between fork length and body area (excluding head and fins). Body tracings were made from photographs of 29 juvenile chinook salmon, and an image analysis program was used to calculate body area. The surface area (AREA) of one side (excluding head and fins) of a juvenile salmon was estimated by: $AREA = 0.13 \ FL^2 - 207.8 \ mm^2$ where FL is fork length measured in millimeters. This relation was used to determine the body areas of the 59 experimentally descaled chinook salmon and the percentages of body area descaled.

Control prey for experiments were anesthesized and held one at a time out of water for 20 s to simulate the handling stress associated with descaling. We alternated between descaling treatment fish and handling control fish to eliminate the effects of differing recovery times.   Following descaling or handling, prey were placed into 100-L aerated tanks and allowed 1 h of recovery before being placed into experimental tanks.

Most experiments were conducted in six indoor 1400-L circular tanks described above (Lucchetti and Gray 1988). Three northern squawfish per tank were used for each trial; fish were starved for 2 d prior to a trial.   Experiments were conducted either over 24 h (1100-1100) with a natural photoperiod, or during a 3 h evening period (1900-2200) with an hour each of light, dusk, and dark.   For the 24 h experiments, 10 descaled and 10 control prey per northern squawfish were initially placed in tanks, and for the 3 h experiments, 5 of each prey type per northern squawfish were used. At the end of an experiment uneaten prey were collected and examined for descaling.   Twelve trials were conducted at each descaling level and experimental duration (a total of 48 trials).

Predation trials were also conducted in a 11,300-L flowing-water raceway (7.6 m long x 1.2 m wide x 1.2 m deep). Temperature was maintained at 17-18°C.   Experiments took place during 3 h evening periods (1900-2200) with an hour each of light, dusk, and dark. Ten northern squawfish per raceway trial were used, after a 2

d starvation period. Five descaled and 5 control prey per northern squawfish were placed into the upstream end of the raceway at the beginning of an experiment; uneaten prey were removed and examined 3 h later. Two raceway trials were conducted using 10% descaled prey, and three trials used 20% descaled prey.

Tanks in which greater than 50% of the prey were consumed were not included in analyses. Results were combined for each of the descaling levels and experimental durations (Figure 1). Observed and expected frequencies of descaled and control prey consumed were compared with a chi-square (X^2) goodness of fit test. Expected frequencies, assuming no selection, were derived assuming a 1:1 ratio of prey types consumed.

Experiments were conducted to assess if 10% and 20% descaling affects survival of juvenile chinook salmon in the absence of predators. Eight groups of 30 fish were used, 2 groups at each descaling level, and 4 groups of control. Fish were treated according to methods previously described and placed into indoor circular tanks. Mortality was monitored over a 24 h period for the 10% descaled fish and a 72 h period for the 20% descaled fish.

Results

Northern squawfish never consumed greater than 50% of the prey in a tank; thus, the results of all trials were included in analyses. The mean percentage of area descaled on one side of a salmon (excluding head and fins) was 26.2% (SD 4.0; n = 59), or 13.1% of the total area. Experiments conducted to test survival of 10% and 20% descaled juvenile salmon in the absence of predators resulted in 100% survival of all descaled and control fish.

In all experiments conducted with 10% descaled salmon, and during experiments using 20% descaled prey in the raceway, 48-51% of consumed prey were descaled (Figure 1), which did not differ significantly (P>0.05) from the expected frequency. Only during experiments conducted in the circular tanks with prey descaled at the 20% level were slightly more (about 60%) descaled than control fish consumed (Figure 1), although these results were also not significant $(X^2 = 3.04;$ P $\approx$ 0.08).
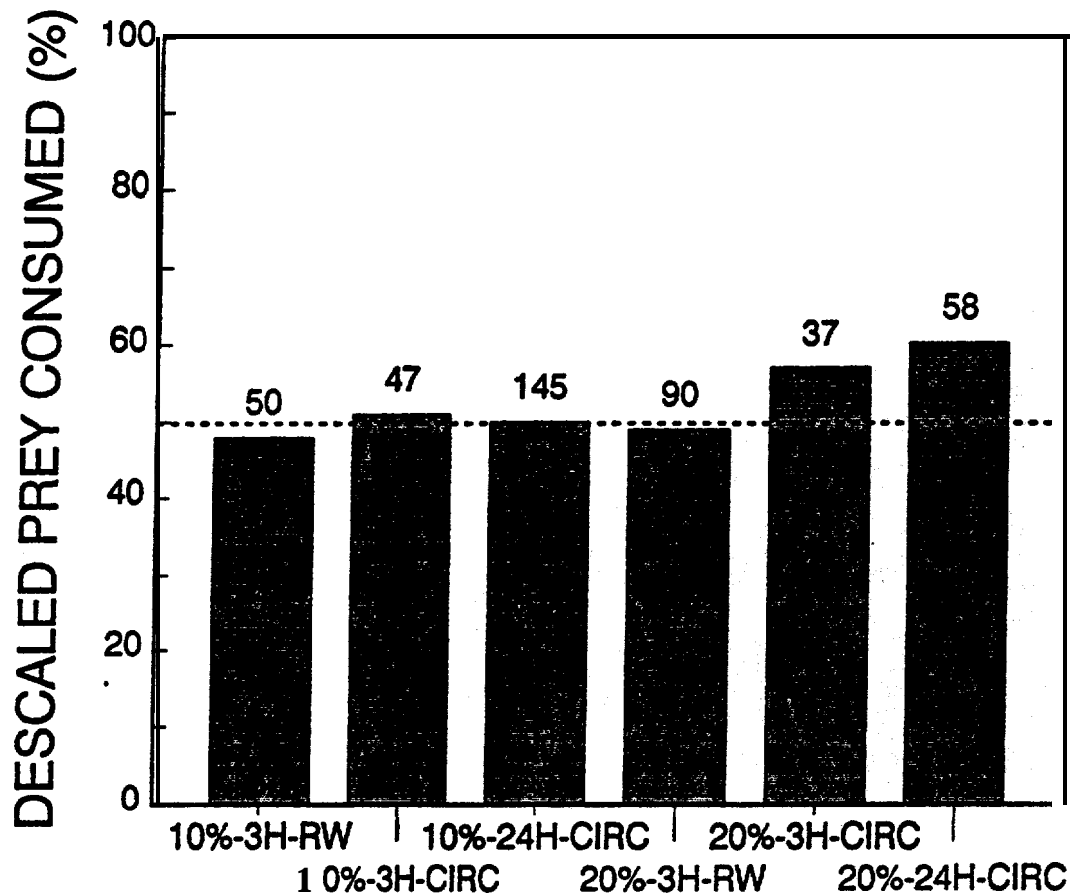
Figure 1. Percentages of descaled juvenile chinook salmon consumed by northern **squawfish** when offered **equal** numbers of control and descaled individuals. Salmon were descaled either on 10% **or** 20% of their total body area. Experiments were conducted either **for** 3 h or 24 h in 1400-L circular tanks **(circ)** or in a 11,300-L raceway (RW). Trial results are combined for each experiment type; numbers above bars are total numbers of control and descaled prey consumed. The horizontal dashed line represents the initial percentage (50%) of descaled prey available.

Discussion

Descaled juvenile chinook salmon were not significantly more vulnerable than control fish to predation by northern squawfish, and did not have a higher mortality rate in the absence of predation. This was true at all levels of descaling tested; designed levels were 10% and 20% of a fish's body area, but in reality these values were somewhat higher, 13% and 26%. Although not significant, more salmon descaled at the 20% level were consumed than control prey during experiments conducted in the circular tanks (Figure 1), perhaps indicating that higher descaling levels than tested could result in increased vulnerability to predation. The levels of descaling we examined are representative of descaling that may take place as a juvenile salmonid passes through one dam (Koski et al. 1990). Fish may be descaled over a greater percentage of their body due to the cumulative effects of migration down the Columbia River through multiple dams (Schoeneman et al. 1961; Raymond 1988).

The results of our experiments indicate that descaling is not detrimental under the tested conditions. In the field, however, other factors must be considered. Scale loss is often accompanied by other types of physical damage (Kostecki et al. 1987). Descaled fish may be more susceptable to stress (M Mesa, USFWS, unpublished data) and disease, which in combination could result in enhanced predation risk or mortality. Damage to the skin, scale, and slime complex disrupts the osmoregulatory ability of a fish; Bouck and Smith (1979) found that removal of 25% of the slime and scales from the bodies of juvenile coho salmon resulted in no deaths in fresh water, but 75% mortality in seawater. The long and short-term effects of descaling may differ, particularly as scales regenerate. Bouck and Smith (1979) noted that 90% of coho salmon regained their tolerance to seawater after 24 h in fresh water. In our study, however, there was no difference in results between experiments conducted over 3 h versus 24 h.

In conclusion, although descaling at low levels may not cause increased mortality or vulnerability of a fish to predation, descaling at higher levels or combined with other factors may have detrimental effects that should not be overlooked. Little research concerning the effects of descaling has been conducted; additional studies are needed to fully understand its long and short-term consequences.

Acknowledgments

References

Black, E. C., and S. J. Tredwell. 1967. Effect of a partial loss of scales and mucous on carbohydrate metabolism in rainbow trout (<u>Salmo uairdneri</u>). Journal of the Fisheries Research Board of Canada 24: 939-953.

Bouck, G. R., and S. D. Smith. 1979. Mortality of experimentally descaled smolts of coho salmon (<u>Oncorhynchus kisutch</u>) in fresh and salt water. Transactions of the American Fisheries Society 108: 67-69.

Gessel, M H., J. G. Williams, D. A. Brege, and R. F. Krcma. 1991. Juvenile salmonid guidance -at the Bonneville Dam second powerhouse, Columbia River, 1983-1989. North American Journal of Fisheries Management 11: 400-412.

Koski, C. H., S. W Pettit, and J. L. McKern. 1990. Fish transportation oversight team annual report - FY 1989. Transport operations on the Snake and Columbia Rivers. NOAA Technical Memorandum NMFS F/NWR-27.

Kostecki, P. T., P. Clifford, S. P. Gloss, and J. C. Carlisle. 1987. Scale loss and survival in smolts of Atlantic salmon (<u>Salmo salar</u>) after turbine passage. Canadian Journal of Fisheries and Aquatic Sciences 44: 210-214.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River Basin. North American Journal of Fisheries Management 8: 1-24.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120: 448-458.

Schoeneman, D.E., R.T. Pressey, and C.D. Junge. 1961. Mortalities of downstream migrant salmon at McNary Dam Transactions of the Amerian Fishery Society 90: 58-72.

Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? Ecology 68: 669-674.

Van Oosten, J. 1957. The skin and scales, p. 207-244, <u>In</u> M E. Brown (ed.) The physiology of fishes. Vol. 1. Academic Press New York, NY.

Report 4

Effects of Multiple Acute Disturbances on the Predator Avoidance, Physiology, and Behavior of Juvenile Chinook Salmon

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Abstract

I examined the predator avoidance, physiological, and behavioral effects of two multiple acute stressors (handling and physical agitation) on juvenile spring chinook salmon Oncorhynchus tshawytscha. Both stressors elicited lethargic behavior in the fish, but the agitation stress also caused disorientation and occasional injury. When equal numbers of stressed and unstressed fish were exposed to predation by northern squawfish Ptychocheilus oregonensis Tfor various lengths of time (1-24 h), only fish receiving the agitation stress and exposed to predation $\leq$ lh showed a significant increase in their vulnerability to predation. Because of time constraints in analyzing samples, data on the physiological responses of juvenile salmon to the imposed stressors will not be presented in this report. My results suggest that there are several aspects to consider in the conduct and interpretation of predation tests designed to assess the effects of stress. Observed responses are likely polymorphic and dependent on the stressor itself, the predator-prey system being studied, and experimental protocols.

Introduction

Because of routine aquacultural practices and extended seaward migrations, juvenile Pacific salmon Oncorhynchus SDD. are commonly subjected to multiple stresses. For example, fish in hatcheries are often crowded, handled, and then subjected to measurement or marking procedures. Also, juvenile salmon passing through dams are subjected to-distinct elements (e.g. traveling screens, gatewells, fish sorters) of the collection system that can have cumulative stress effects on the fish (Matthews et al. 1986; Maule et al. 1988). Until recently, the physiological and behavioral effects of

multiple stresses have received little attention, even though it is generally accepted that stresses rarely occur in isolation (Leatherland and Sonstegard 1984). To date, several studies have assessed the effects of multiple disturbances using a variety of stressors (Barton et al. 1986; Pickering and Pottinger 1987; Peters et al. 1988; Sigismondi and Weber 1988; Jarvi 1989; Mesa and Schreck 1989). Although these studies show that multiple disturbances elicit severe physiological and behavioral stress responses, the effects on a ecologically relevant behavior such as predator avoidance remain unknown.

Several studies have shown increased vulnerability to predation of prey exposed to a variety of isolated stressors, including temperature shock (Coutant 1973; Yocum and Edsall 1974), contaminants (Hatfield and Anderson 1972; Kania and O'Hara 1974), and handling (Olla and Davis 1989). Sigismondi and Weber (1988) speculated that the likely consequences for juvenile spring chinook salmon O. tshawtscha exposed to multiple acute handling stresses are increased exposure and vulnerability to predation or other environmental hazards. Because of the cumulative, relatively severe effects of multiple stresses, it is conceivable that deficits in predator avoidance would be more pronounced and longer lasting. Evaluating changes in both performance and physiology of fish should lead to a better appraisal of their overall condition after exposure to stress (Schreck 1981; Wedemeyer and McLeay 1981; Beitinger 1990).

The objective of this study was to evaluate the predator avoidance and physiological effects of two multiple, acute stressors (handling and physical agitation) on juvenile chinook salmon. The type of handling used was representative of stressors that are well known to elicit characteristic stress responses in fish (Barton et al. 1986). The physical agitation was a new procedure designed to simulate a disorienting, physically demanding environment perhaps not unlike that encountered by fish during dam passage. I conducted bioassays of performance by exposing groups of stressed and unstressed fish to predation by northern squawfish Ptychocheilus oregonensis to assess any differences in survival between the two groups. I assessed the primary or endocrine response to stress on the basis of plasma cortisol concentrations, and the secondary or metabolic response of plasma glucose. The data were also used to evaluate any possible correlation between clinical indicators of stress and predator avoidance ability.

Methods

Test fish.-Subyearling spring chinook salmon (average weight $\pm$ SE, 10.8 $\pm$ 0.2 g) from the Little White Salmon National Fish Hatchery were used in all experiments. Fish were maintained in 0.6-m diameter circular, flow through tanks receiving well water at temperatures similar to those used in predation experiments (12-18°C). Fish were fed ad libitum twice daily with commercial moist feed and held under natural photoperiod. They were acclimated for at least two weeks before all experiments.

Northern squawfish (>275 mm FL), collected from the Columbia River by electroshocking, were used as predators for all experiments. Fish were acclimated in a large raceway tank (see Petersen et al. 1990 for a complete description) for up to 3 weeks prior to experiments. During the acclimation period and between experiments, northern squawfish were fed a maintenance diet of live juvenile coho salmon Q. kisutch. I judged acclimation to be complete when fish were consistently feeding at a high rate.

Predation experiments.-Prior to all trials, chinook salmon were graded by size, cold branded on either the right or left side or marked with an adipose fin clip, and held separately for at least two weeks to allow recovery. Prior to a trial, a sample (Table 1) of chinook salmon from each marked group were transferred to and held separately in the aluminum holding tank. One group was randomly designated as the treatment (stressed) group; the other group served as controls. All fish were acclimated for up to 72 h and maintained as described previously. Ten northern squawfish were used in all experiments. During the 6 and 24 h multiple handling stress experiments, individual northern squawfish were used for a maximum of two trials. For all other experiments, I used predators for up to 3 months. Experiments were conducted from May-November, 1989-1991.

To begin an experiment, predators were starved for 24-72 h prior to introduction of the prey. Following predator starvation, the group .of prey designated as treatment fish were subjected to either three handlings, each 1 h apart or three agitations, each 0.5 h apart. The handling stress consisted of rapidly (< 60 s) netting the fish from the tank, holding them in the air for 30 s, and returning them to the tank. The agitation stress consisted of filling a 19 L bucket about 1/2 full with water, transferring fish from the aluminum tank to the bucket, and pouring the fish into another bucket on the floor; water fell a distance of

Table 1.-Experimental design used to evaluate differential predation by northern squawfish on juvenile chinook salmon subjected to two stressors.   MHS = multiple handling stress; MAG = multiple agitation stress.

Stressor	Experiment Duration	Number of Replicates	Number of Prey Released	
			Stressed	Control
MHS	24 h	3	40	40
	6 h	3	40	40
	3 h	5	20	20
	90 min	5	20-40"	20-40"
	60 min[b]	6	20	20
MAG	60 min[b]	11	20	20

'Number of prey released varied due to unusually high predation rates

[b]Experiments ran until about 30-50% of the prey were eaten or for 60 min, which ever came first.

about 1.0 m.   The buckets were then switched and the process continued for 5 min before returning the fish to the aluminum tank. For most experiments, at 5 min after the final stress, 5-10 fish from each group were netted and immediately placed in a lethal dose of MS-222.   The fish were then removed from the anaesthetic and-bled into an ammonium heparinized capillary tube after severance of the caudal peduncle.   Plasma was obtained by centrifugation and stored at -15°C for future assay.   Immediately following removal of fish for blood samples, we removed the aluminum tank divider and allowed the remaining control and treatment fish to mix briefly; they were then released into the raceway by removing standpipes. For early experiments, predation was be allowed to proceed for 1.5-24 h (Table 1); during later experiments, predation continued until 30-50% of the total prey released were eaten or for 1 h, which ever came first.   Because preliminary experiments showed that northern squawfish fed better in low light conditions, all experiments were initiated during a simulated evening crepuscular period. Experiments lasting from 1.5-24 h had some of the time period spent in complete darkness.   At the end of all experiments, all surviving prey were netted from the raceway and identified.

Data from the 6 and 24 h handling stress trials were pooled for analysis.   The data from other experiments were also pooled, but were first subjected to a heterogeneity chi-square analysis to determine if the replicates were homogenous (Sokal and Rohlf 1981). Chi-square goodness-of-fit tests were used on pooled data to test the hypothesis that feeding was random (i.e. 50:50).

Physiological experiments -To assess the physiological effects of the multiple handling stresses, fifty juvenile chinook salmon were maintained in each of eight, 0.6-m diameter circular tanks randomly assigned to one of four treatments: (1) a single handling; (2) two handlings separated by 1 h; (3) three handlings, each 1 h apart; or (4) undisturbed controls. This design resulted in two replicate tanks per treatment and is similar, except for the time separating stresses, to protocols of Barton et al. (1986).   To evaluate the multiple agitation procedure, fifty fish were maintained in each of four tanks, two tanks receiving multiple agitations as described above and two serving as undisturbed controls.   All fish were acclimated for at least two weeks prior to experiments.   Water temperature was 12-13°C and flourescent lights with timers simulated ambient photoperiod.   Blood samples ($\underline{N}$ = 10 per time period) were collected as described previously from fish just before each stress, and at 0.5, 1, 3, 6, 12, 24, and 168 h after the final stress.   The handling experiment was conducted on August 7-8, 1989 and the agitation experiment on August 15, 1991.

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Plasma cortisol was determined by ^{3}H-radioimmunoassay (Foster and Dunn 1974), as modified by Redding et al. (1984) for use with salmonid plasma. Plasma glucose was measured using a biochemistry analyzer (Yellow Springs Instruments Inc., Model 2700D). All data were tested for homogeneity of variance (Bartlett's test, Sokal- and Rholf 1981). Those found to. be homogenous were treated by analysis of variance followed by Fisher's Least Significant Difference Test at the 5% probability level (Ott 1977). Data with heterogeneity among the means were either transformed to stabilize the variance or subjected to a Kruskal-Wallis One-Way Analysis by Ranks (Sokal and Rholf 1981).

Results

Predation experiments.-Although prey subjected to multiple handling stresses were lethargic, there was little evidence for northern squawfish differential predation, regardless of experiment duration (Figure 1). For all experiments, predation was occuring at random (Table 2). Heterogeneity analysis showed that the replicates within different experiments were homogenous (Table 2).

Prey subjected to multiple agitations were lethargic, frequently disoriented, occasionally injured, but never died. The replicate experiments showed no significant heterogeneity, and the pooled data revealed that stressed fish were eaten in significantly greater numbers than control fish (Table 3).

Physioloaical experiments.-Results not available.
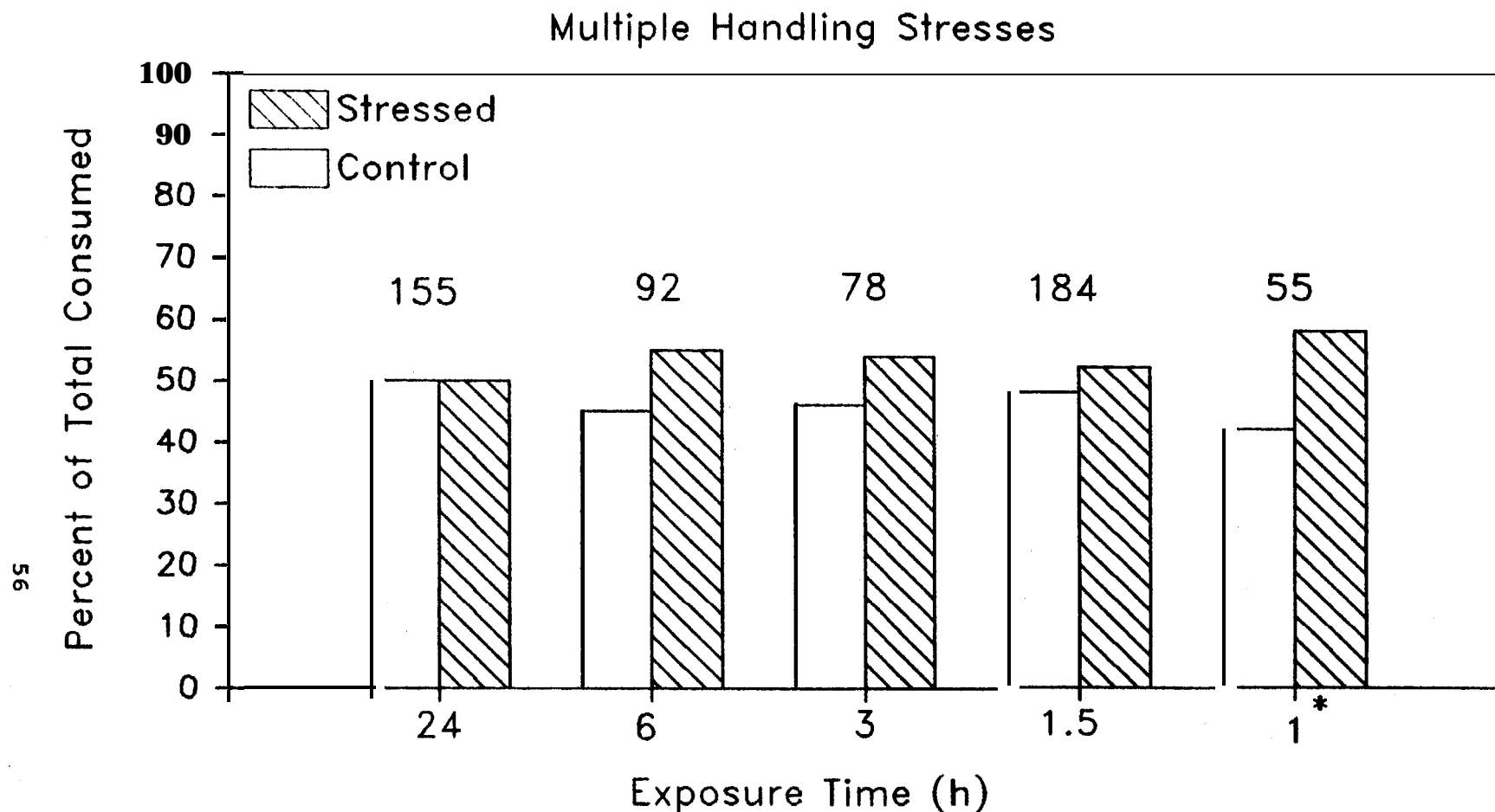
Multiple Handling Stresses

Figure 1.—Percentage of the total number of juvenile chinook salmon eaten by northern squawfish that were either stressed or controls. Numbers above each pair of bars are the total number of fish consumed, all replicates combined. Asterisk denotes that these experiments ran until 30–50% of the prey were consumed, or for 1 h.

		Number Eaten		Percent Eaten of Total			
Duration	Replicate	Stress	Control	Released	Test	df	x^2
24 h	1	34	34	68			
	2	22	19	51			
	3	22	24	70			
	Σ	78	77		Pooled	1	0.006
6 h	1	34	29	79			
	2	5	4	12			
	3	12	8	25			
	Σ	51	47		Pooled	1	1.087
3 h	1	12	9	53		1	0.429
	2	7	5	30		1	0.333
	3	13	11	62		1	0.167
	4	17	12	91		1	0.862
	5	10	11	53		1	0.048
					Total	5	1.838
	Σ	59	48		Pooled	1	1.131
					Heterogeneity	4	0.707

Table 2.--Results of differential predation tests for juvenile chinook salmon subjected to the multiple handling stresses. All chi-square tests of random (50:50) feeding were not significant ($p > 0.05$).

Table 2, cont.

Duration	Repl	Number Eaten Control	Number Eaten Stress	Percent Eaten of Total Released	Test	df	x^2
90 min	1	12	12	60		1	0.000
	2	16	14	75		1	0.133
	3	21	19	71		1	0.100
	4	25	24	61		1	0.020
	5	20	18	54		1	0.105
					Total	5	0.359
	Σ	94	87		Pooled	1	0.271
					Heterogeneity	4	0.088
60 min[a]	1	5	2	18			
	2	6	6	30			
	3	8	8	40			
	4	8	4	30			
	5	1	1	2			
	6	4	2	6			
	Σ	32	23		Pooled	1	1.473

[a]Experiments ran until about 30-50% of the prey were eaten, or for 60 min, whichever came first.

Table 3.—Results of differential predation experiments for juvenile chinook salmon subjected to multiple agitation stresses. Asterisks denot. predation, rates that differ significantly from random (50:50). $P < 0.05$, $P < 0.01$, P to.001

Replicate	Number Eaten Stress	Number Eaten Control	Percent Eaten of Total Released	Test	df	χ^2
1	12	0	33		1	12.000-
2	8	2	30		1	3.600*
3	9	4	33		1	1.923
4	13	4	43		1	4.765*
5	8	6	35		1	0.286
6	7	6	33		1	0.077
7	6	7	33		1	0.077
8	15	6	53		1	3.857*
9	10	3	33		1	3.769*
10	7	8	38		1	0.067
11	3 2	9	55		1	0.429
				Total	11	30.840"
Σ	107	55		Pooled	1	16.691***
				Heterogeneity	10	14.149

Discussion

Because several key pieces of information were not available for this report, only a brief discussion of the results will be presented. Experiments and analyses which need to be completed include: (1) more replicates of the short term (i.e. 30-50% eaten or for 60 min) predation experiment assessing the effects of multiple handling stresses; (2) plasma cortisol titers of fish just prior to release to predators; and (3) the endocrine and metabolic stress responses of the juvenile chinook salmon. Because these pieces of information could potentially change some of my results, this report should be considered only an update of progress. The experiments reported here suggest that behavioral bioassays of predator-prey interactions can be used to assess the effects of stress on fish. Such experiments have obvious ecological significance and are often mentioned, yet still receive little attention when compared to physiological assessments of stress on fish (Wedemeyer et al. 1991). My results suggest that there are several aspects to consider in the conduct and interpretation of predation tests designed to assess the effects of stress. Observed responses are likely polymorphic and dependent on the stressor itself, the predator-prey system being studied, and experimental protocols and statistical procedures. I believe the effects of stressors that elicit disorientation and fatigue may provide insight into dam passage related stress and the potential for differential predation by northern squawfish in the dam tailraces. Such information might question the overall impact of predation as a mortality factor of juvenile salmon and should lead to more informed management decisions aimed at increasing salmonid survival.

References

Barton, B.A., C.B. Schreck, and L.A. Sigismondi. 1986. Multiple acute disturbances evoke cumulative physilolgical stress responses in juvenile chinook salmon. Transactions of the American Fisheries Society 115:245-251.

Beitinger, T.L. 1990. Behavioral reactions for the assessment of stress in fishes. Journal of Great Lakes Research 16:495-528.

Coutant, C.C. 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. Journal of the Fisheries Research Board of Canada 30:965-973.

Foster, L. B., and R. T. Dunn. 1974. Single-antibody technique for radioimmunoassay of cortisol in unextracted serum or plasma. Clinical Chemistry 20:365-368.

Hatfield, C. T., and J.M. Anderson. 1972. Effects of two insecticides on the vulnerability of atlantic salmon (<u>Salmo salar</u>) parr to brook trout (<u>Salvelinus fontinaliq</u>) predation. Journal of the Fisheries Research Board of Canada 29:27-29.

Jarvi, T. 1989. Synergistic effect on mortality in atlantic salmon, <u>Salmo salar</u>, smolt caused by osmotic stress and presence of predators. Environmental Biology of Fishes 26: 149-152.

Kania, H.J., and J. O'Hara. 1974. Behavioral alterations in a simple predator-prey system due to sub-lethal exposure to mercury. Transactions of the American Fisheries Society 103:134-136.

Leatherland, J.F., and R. A. Sonstegard. 1984. Pathobiological responses of feral teleosts to environmental stressors: interlake studies of the physiology of Great Lakes salmon. Pages 115-149 <u>in</u> V. W Cairns, P. V. Hodson, and J.O. Nriagu, editors. Contaminant effects on fisheries. John Wiley and Sons, New York.

Matthews, G. M, D. L. Park, S. Achord, and T. E. Ruehle. 1986. Static seawater challenge test to measure relative stress levels in spring chinook salmon smolts. Transactions of the American Fisheries Society 115:236-244.

Maule, A. G., C. B. Schreck, C. S. Bradford, and B. A. Barton. 1988. Physiological effects of collecting and transporting emigrating juvenile chinook salmon past dams on the Columbia River. Transactions of the American Fisheries Society 117:245-261.

Mesa, M G., and C. B. Schreck. 1989. Electrofishing mark-recapture and depletion methodologies evoke behavioral and physiological changes in cutthroat trout. Transactions of the American Fisheries Society 118:644-658.

Olla, B. L., and M W Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (<u>Oncorhynchus kisutch</u>) juveniles. Aquaculture 76:209-214.

Ott, L. 1977. An introduction to statistical methods and analysis. Duxbury Press, North Scituate, Massachusetts.

Peters, G., M Faisal, T. Lang, and I. Ahmed. 1988. Stress caused by socal interaction and its effect on susceptibility to Aeromonas hydrophilg infection in rainbow trout Salmo oairdneri. Diseases of Aquatic Organisms 4:83-89.

Redding, J.M., C. B. Schreck, E. K. Birks, and R. D. Ewing. 1984. Cortisol and its effects on plasma thyroid hormone and electrolyte concentrations in fresh water and during seawater acclimation in yearling coho salmon, Oncorhynchus kisutch. General and Comparative Endocrinology 56:146-155.

Schreck, C. B. 1981. Stress and compensation in teleostean fishes: response to social and physical factors. Pages 295-321 in A. D. Pickering, editor. Stress and fish. Academic Press, New York, New York.

Sigismondi, L. A., and L. J. Weber. 1988. Changes in avoidance response time of juvenile chinook salmon exposed to multiple acute handling stresses. Transactions of the American Fisheries Society 117:196-201.

Sokal and Rohlf. 1981. Biometry. W H. Freeman and Co., New York. Specker, J. L., and C. B. Schreck. 1980. Stress responses to transportation and fitness for marine survival in coho salmon (Oncorhynchus kisutch) smolts. Canadian Journal of Fisheries and Aquatic Sciences 37:765-769.

Wedemeyer, G. A. and D.J. McLeay. 1981. Methods of determining the tolerance of fishes to environmental stressors. Pages 247-275 in A. D. Pickering, editor. Stress and Fish. Academic Press, New York, New York.

Wedemeyer, G.A., B. A. Barton, and D.J. Mcleay. 1991. Stress and acclimation. Pages 451-489 in C. B. Schreck and P. B. Moyle, editors. Methods for Fish Biology. American Fisheries Society, Bethesda, Maryland.

Yocum, T. G., and T. A. Edsall. 1974. Effect of acclimation temperature and heat shock on vulnerability of fry of lake whitefish (Coreaonus clupeaformis) to predation. Journal of the Fisheries Research Board of Canada 31:1503-1506.

Report 5

Prolonged Swimming Performance of Northern Squawfish: Can Water
Velocity be used to Reduce Predation on Juvenile Salmonids at
Columbia River Dams?

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Abstract

We determined the prolonged swimming performance of two sizes
of northern squawfish Ptychocheilus ooregonensis at 12 and 18°C.
Swimming performance was positively related to fish size and water
temperature. For medium size fish (30-39 cm fork length), the
velocity at which 50% of the fish fatigued (FV50) ranged from 95-105
cm/s and maximum performance from 107-112 cm/s. For large fish (40-
49 cm), FV50 ranged from 100-114 cm/s and maximum performance from
118-135 cm/s. We found a significant amount of inter-individual
variability in performance. The number of fish that did not swim
increased directly with velocity and may have been affected by fish
size, although our analysis was equivocal. The number of fish that
did not swim was inversely related to water temperature, but not
significantly so. Our results suggest that high water velocity
areas may be used to exclude or reduce predation by northern
squawfish around juvenile salmonid bypass outlets at Columbia River
dams, especially during spring and early summer. We estimate that
northern squawfish would not be able to hold station at water
velocities above 150 cm/s. We recommend the construction of new or
modification of existing bypass facilities include an area of high
water velocity around the outlet, provide few eddies and minimal
submerged cover, and be located away from littoral areas.

Introduction

The northern squawfish Ptychocheilus oreaonensis is known to be
a major predator on juvenile salmonids in a variety of waters
(Ricker 1941; Jeppson and Platts 1959; Thompson and Tufts 1967;
Uremovich et al. 1980; Poe et al. 1991). In the Columbia River,
predation by northern squawfish on juvenile salmonids is most

intense in the tailrace areas behind dams (Petersen et al. 1990; Poe et al. 1991), a scenario accurately predicted for riverine systems by Brown and Moyle (1981). Predation near dams is severe because of a high concentration of prey near bypass outfalls that may show deficits in predator avoidance because of passage related disorientation, stress, and injury (Matthews et al. 1986; Maule et al. 1988).

Concern over the decline of many stocks of Pacific salmon Oncorhynchus spp. has led to efforts aimed at increasing juvenile salmonid survival, including a reduction in predation related mortality. Although predator removal efforts are currently being used in the Columbia River to reduce predation (Nigro et al. 1990), it is conceivable that other methods designed to protect juvenile salmon as they outmigrate might be as efficient, ecologically more prudent, and less costly. One general method to protect juvenile salmonids that is receiving much attention is the location, alteration, and design of existing or planned bypass facilities. Because northern squawfish seemingly prefer low water velocity areas around bypass outlets (Faler et al. 1988), this question becomes salient: can water velocity be used to exclude or reduce the efficiency of predators around bypass outfalls? Although Faler et al. (1988) found that radio-tagged northern squawfish were not located in water velocities > 70 cm/s, their study was not designed to assess swimming performance and lacks the precision necessary to fully address the above question.

Although the swimming performance of many fishes have been well documented (see reviews by Beamish 1978 and Videler and Wardle 1991), Berry and Pimentel (1985), who studied the performance of the congeneric Colorado squawfish P. lucius, stated that the use of these data to predict the capabilities of unstudied species may be questionable. Our objective, therefore, was to determine the performance of northern squawfish at prolonged swimming speeds, i.e. those speeds that a fish can maintain for $\leq$ 200 min and typically end in fatigue (Beamish 1978). We also assessed the effects of fish size, water temperature, and sex on swimming performance. This information, coupled with river discharge and velocity data under various flow regimes, should provide much needed biological criteria to aid in the siting and operation of juvenile fish bypass systems.

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Methods

Northern squawfish were captured by electrofishing from the Columbia River and transported to our laboratory. They were held under natural photoperiod in circular tanks (1.2 m diameter, 0.8m deep) that received well water heated to $\pm$ 1°C of the selected experimental temperature. Water flow in the tanks provided enough current for orientation. All fish were acclimated at least one week prior to testing and were fed in excess with live juvenile coho salmon O. kisutch.

Swimming performance was measured in a stamina tunnel similar to that used by Thomas et al. (1964) and Berry and Pimentel (1985). Briefly, the tunnel consisted of two 500 L reservoirs connected by two Plexiglas pipes, one a return-flow pipe and the other a 20-cm-diameter, 2 m long swimming chamber. We used a flow meter to determine tunnel water velocities (cm/s) at different pump speeds (hertz) by adjusting flows with a frequency drive that varied pump speed. Resulting data were analyzed using linear regression and we calculated desired pump speeds by inserting a test velocity into the equation:

Pump speed (hertz) = 0.381 + 0.533(Velocity)
R^2 = 99.94; P < 0.0001

Fish were encouraged to swim by electrified screens (5-10 V AC) located at each end of the swimming chamber. The upstream screen kept fish from holding station at the tunnel entrance, whereas the downstream screen was used to encourage tiring fish to swim About 1.5 m of the middle of the swimming chamber was wrapped with black plastic except for the top to allow entrance of light from above. This isolated the fish and provided an aid for orientation.

Although the swimming speed of fish tested in tunnels is subjected to various influences (Webb 1975), we felt that, following the reasoning of Williams and Brett (1987), solid blocking was the only significant factor requiring correction. We first determined the cross-sectional area of a sample of fish (N = 37) by cutting a fish at its thickest point, stamping the impression on blank paper, and measuring area with a digitizer. We then assessed the relation between cross-sectional area and weight using linear regression and predicted cross-sectional area of test fish by

XC-area (cm^2) = 17.8 + 0.033 (weight) R^2 = 94.17; P < 0.0001.

Because 98% of our fish exceeded 10% of the cross-sectional area of the tunnel, we calculated corrected swimming velocities using the formula (Bell and Terhune 1970)

$V_F = V_T (1 + (t(n)(A_o/A_t)^{1.5}$, where $V_F =$ corrected velocity, $V_T =$ test velocity, $t = 0.8$, $n = 0.7$ length/thickness, $A_o =$ maximum cross-sectional area of fish, and $A_t =$ tunnel Goss-sectional area.

Northern squawfish performance was assessed at $12°C$ and $18°C$ for medium (30-39 cm FL) and large (40-49 cm FL) size fish. These temperatures represent the average water temperature in the Columbia River during the spring and summer juvenile salmonid out-migrations. We used a test protocol similar to that of Berry and Pimentel (1985). The day before testing, three randomly sized northern squawfish were transferred to a tank that had water velocity of about 30 cm/s. Food was withheld from these fish to minimize the effect of feeding on standard metabolism (Beamish 1964; Bernatchez and Dodson 1985). The next morning, the tunnel was filled with water at the acclimation temperature of the fish. A single fish was netted from the tank, fork length (FL) rapidly measured to the nearest cm, and placed into the swim chamber. Fish were allowed to acclimate for 30 min at a water velocity of 0.75 fork lengths per second (FL/s). Following acclimation, the water velocity was gradually increased over about 5 min to a selected test velocity. Selected test velocities were determined from preliminary experiments designed to find a range of velocities over which the percent of fish fatigued varied from 0 to 100% in a 120 min. Fish were tested for 120 min or until fatigued; sample size varied at each test velocity. We defined a fish as fatigued when it became impinged on and would not leave the downstream screen despite continuous shocks. Fish that showed erratic behavior during the gradual acceleration and did not swim were weighed and measured, sexed, but excluded from the tests. Immediately following a test, each fish was removed, killed by a blow to the head, weighed to the nearest 25 g, and sex determined. A blood sample was taken by cardiac puncture to determine plasma glucose and lactate levels (data not available for this report).

We used a "dose-response" curve to describe the relation between percent fatigued and velocity for both size groups and for males and females (Brett 1967). Because our curves were not complete, we estimated FV, , values (the velocity at which 50% of the fish fatigued) and maximum prolonged performance by graphical interpolation. We compared the mean lengths of males and females using a two-sample i-test and the mean lengths of fish that did not fatigue, fish that fatigued, and those that did not swim by one-way analysis of variance (ANOVA) followed by Fisher's least-significant-difference test at the 5% probability level (Ott 1977). Chi-square

analysis was used to determine if the number of fish that did not swim was independent of temperature.

Results

Northern squawfish fatigued faster at 12°C than at 18°C, irrespective of size (Figure 1). The estimated FV,, values were 10-12 cm/s lower at 12°C than at 18°C. Estimated maximum performance ranged from about 107-112 cm/s for medium size fish and from 118-135 cm/s for large fish, depending on temperature. Although small fish swam relatively faster than large fish when speed was expressed in FL/s, absolute swimming speed (cm/s) was positively related to fish size.

Females comprised 85% of the 189 fish tested. Because of low sample sizes for males, a comparative description of performance between sexes was untenable. Females were significantly larger than males (Table 1). For both size groups, the number of fish that did not swim was positively related to velocity (Figure 2). For medium size fish, we found no significant size difference among fish that did not fatigue, fish that fatigued, and those that did not swim at either temperature (Table 2). For large fish at 12°C, fish that fatigued were significantly larger than both other categories (F = 7.625; P = 0.0016). At 18°C, fish that did not fatigue were significantly smaller than both other categories (F = 4.44; P = 0.01).

For both size groups, the percentage of all fish tested . that did not swim decreased inversely with temperature (Table 3) but not significantly so (medium chi-square = 0.86, P = 0.35; large: chi-square = 3.20, P = 0.074).
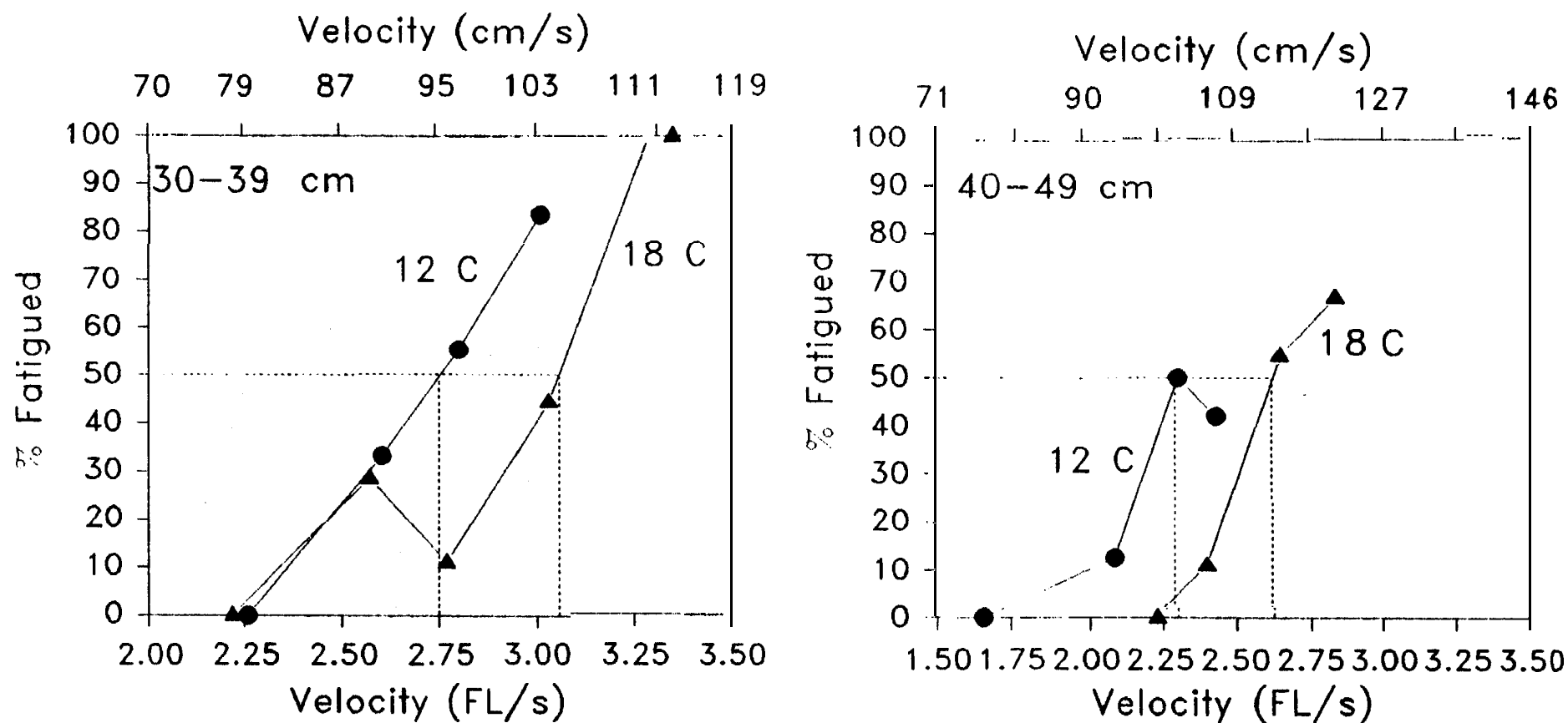
Figure 1.—Relation between percent of fatigued fish and water velocity at 12 and 18 C for two sizes of northern squawfish. The 120 min FV50, or velocity at which 50% of the fish were fatigued in 120 min, is shown by the dashed lines.
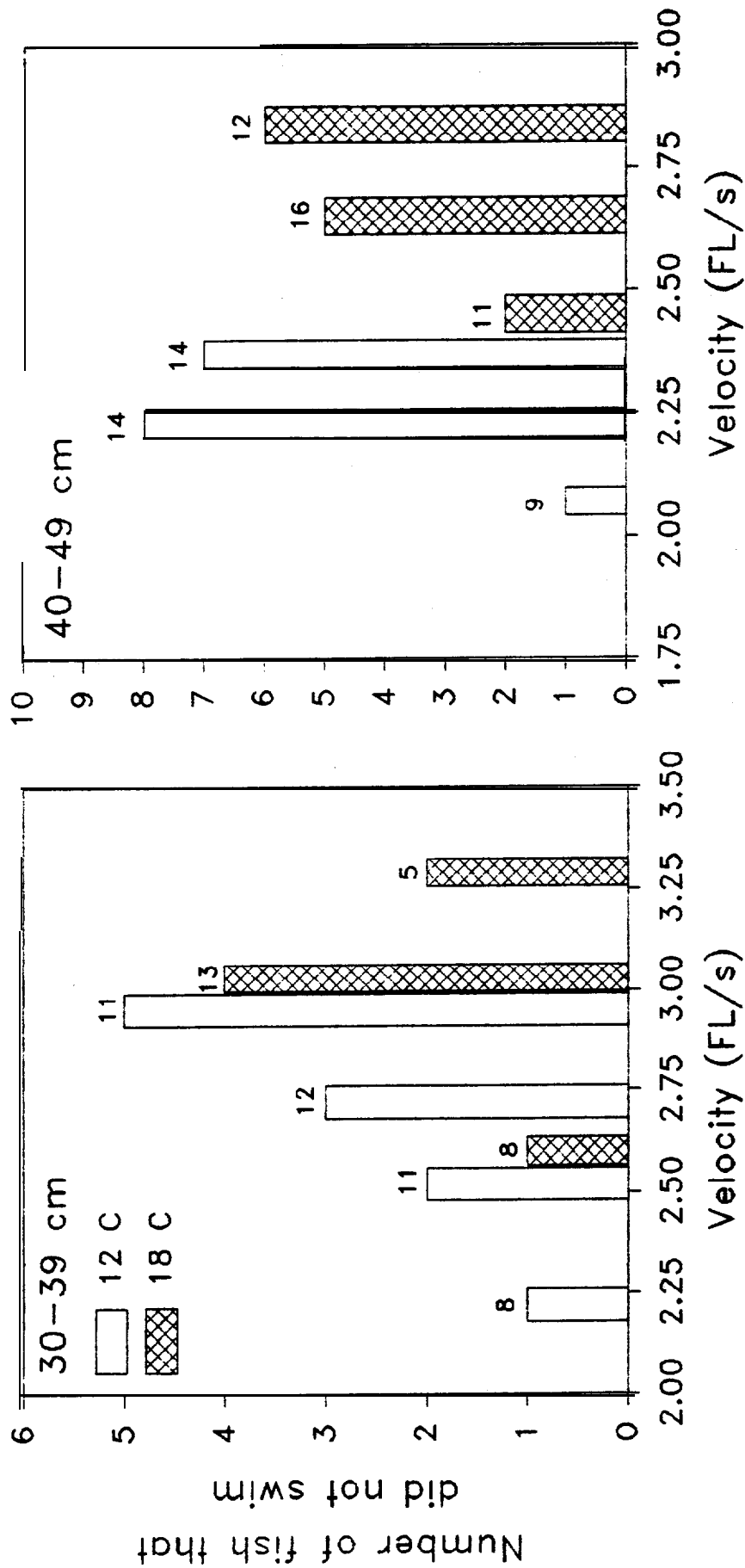
Figure 2.—Number of northern squawfish of two sizes that did not swim at fixed velocities during the gradual acceleration phase of swimming performance tests at 12 and 18 C. Numbers above each bar indicate the total number o ish ested at that velocity.

Table I.-Mean (and SE) fork lengths and weights of male and female northern squawfish used in swimming performance tests.

Sex	N	Lenath (cm)	Weight (g)
Male	24	34 (0.65)	450 (30)
Female	165	40 (0.35)	782 (21)

Table 2.   The number and mean (SE) fork lengths of northern squawfish that did not fatigue, fatigued, or did not swim for two size groups and water temperatures during swimming performance tests. Means within a row with no letters in common are significantly different ($p < 0.05$)'; rows with no letters shown indicate no difference among the means.

		Swimming cateaory					
		Did not fatisue		Fatiaued		Did not swim	
Size group	Temper-ature(°C)	N	Length	N	Length	N	Length
Medium	12	28	35.6(0.40)	13	36.1(0.60)	12	36.0(0.75)
	18	31	34.4(0.49)	11	36.0(0.83)	7	35.6(1.04)
Large	12	18	42.3(0.54)[a]	7	46.1(0.67)[b]	18	43.1(0.51)[a]
	18	35	42.8(0.31)[a]	11	44.2(0.78)[b]	14	44.6(0.58)[b]

Table 3.-The number (and percent) of northern squawfish that did not swim during the gradual acceleration phase of swimming performance tests.

	Number of fish that did not swim	
Size	12°C	18°C
Medium	12 (23)	7 (14)
Large	18 (42)	14 (23)

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Discussion

Although our relations between velocity and percent fatigued are incomplete (additional data collection will be completed in 1992), the prolonged swimming performance of northern squawfish-was dependent on fish size and water temperature. Our FV,, values, which should be the most precise estimates of performance on such dose-response curves (Goulden 1952), compare favorably with those of the Colorado squawfish at 14 and 20°C (Berry and Pimentel 1985), suggesting that the performance of these congenerics is similar. The preference of Colorado squawfish for large riverine systems (Moyle 1976; Tyus et al. 1984) and their migratory behavior (Tyus 1990) might seemingly confer a swimming performance advantage when compared to the typically lacustrine dwelling northern squawfish (Scott and Crossman 1973). Indeed, the life history forms of several species that involve frequent swimming (e.g. extended anadromous migrations) possess greater swimming capabilities than those of more sedentary populations (Tsuyuki and Williscroft 1977; Taylor and McPhail 1985; Taylor and Foote 1991). We suspect that the performance of Colorado squawfish may be significantly underestimated because Berry and Pimentel (1985) used unexercised, hatchery-reared fish and did not correct for solid blocking effects. Because of the similarities in body form between the two congeners and the fact that we used the same swim tunnel as Berry and Pimentel (1985), we were surprised that solid blocking corrections were not applied to their data. It appears that Berry and Pimentel (1985) were mistakenly evaluating cross-sectional diameter and not area, which probably lead to their conclusion that none of their largest fish required correction for solid blocking. Our fish averaged 13% (range: 8-20%) of the area of the swim tunnel and corrected velocities showed an average increase of 17% (range: 8-30%). It seems possible, then, that had Berry and Pimentel (1985) corrected for solid blocking and used fish from their natural habitat, the performance of these two species would better follow their differences in life history traits.

Northern squawfish performed better at 18°C than at 12°C. The swimming performance of fish typically increases with water temperature (Brett 1967; Brett and Glass 1973; Beamish 1978; Glova and McInerney 1977; Bernatchez and Dodson 1985), and peaks at an optimum temperature where physiological functions are most efficient. As temperature increases, fish may have a greater oxygen uptake capacity (Bernatchez and Dodson 1985) or show increases in metabolic rates or enzymatic processes (Brett 1967). Because we only tested performance at 12 and 18°C, the relation between

temperature and performance of northern squawfish remains unclear. Brown and Moyle (1981) stated that northern squawfish prefer water temperatures ranging from 16 to 22°C. Recent studies (Beyer et al. 1988; Vigg and Burley 1991) have shown that consumption and evacuation rates of northern squawfish peak near 21°C. This suggests an optimum temperature for northern squawfish greater than 18°C and that our data probably underestimate their maximum swimming capability.

We were unable to assess the effect of sex on northern squawfish swimming performance because of a significant size-related sexual dimorphism. Male northern squawfish rarely grow larger than 40 cm whereas females may attain lengths greater than 50 cm (Beamesderfer et al. 1987; Petersen et al. 1990). The small number of males tested overall is similar to the 70:30 female/male ratio found in the Columbia River (Petersen et al. 1990). The influence of sex or stage of maturity on swimming performance has received little attention (Beamish 1978). Williams and Brett (1987) found that adult male pink salmon O. gorbuscha were capable of higher swimming speeds than females and that gravid fish performed better than either spawning or spawned out fish. During our tests at 12°C, we noted a large percentage of fish -were gravid and, perhaps not coincidentally, had our highest percentage of fish that did not swim. We suspect that the relatively poor performance of fish at 12°C was due to the combined effects of water temperature and sexual maturity. It is conceivable that species which do not undergo extensive spawning migrations may have less energy available for prolonged performance during sexual maturation.

We noted significant inter-individual variability in performance as evidenced by the high percentage of fish that did not swim. Surprisingly, this type of variability in performance has received only minor attention in swimming studies (Bainbridge 1962; Davis et al. 1963; Brett 1967) even though it can affect the efficiency of tests and provide useful information. For example, we found that the number of fish that did not swim typically increased directly with velocity. Although this may seem intuitively obvious, this type of information is rarely reported and suggests that we were approaching velocities that fish had difficulty coping with. Unlike the fish used by Dorn et al. (1979) and Berry and Pimentel (1985), northern squawfish performed poorly when rapidly subjected to a test velocity. To minimize erratic behavior, we subjected fish to a gradual acceleration (Bainbridge 1962) over a period of about 5 min before reaching the test velocity. We believe this increased the chance of eliciting adequate performance and likely reduced the frequency of fish that did not swim

The reasons for the inter-individual variation are speculative but would presumably have behavioral, morphological, and physiological origins. In our study, we found that a large number of the fish that fatigued or did not swim were commonly on the large end of the size range, although our analysis of size differences was equivocal (Table 2). That larger fish typically performed poorly may simply be an artifact of the size of the swim tunnel. As fish size increased, a greater proportion of the cross-sectioanl area of the tunnel was occupied which perhaps made large fish feel more restrained and less likely to perform adequately. Despite several studies investigating intraspecific variation in locomotor performance of ectothermic vertebrates (Garland and Else 1987; Gleeson and Harrison 1988; Walsberg et al. 1986; Bennett et al. 1989), research of this nature on fish is only just beginning (Kolok, manuscript in review).

Management Implications

Information on the swimming performance of fishes has been used for various management applications, including assessments of the design of fish ladders (Collins et al. 1962; Slatick 1971), water intakes (Dorn et al. 1979), culverts (Jones et al. 1974), and the sublethal effects of pollutants (for a review see Beitinger and McCauley 1990). In the Columbia River, the use of high water velocities to exclude or limit predation by northern squawfish in the area of fish bypass outlets seems promising during the spring and early summer outmigrations. During this time, water temperatures are low, flows are high, consumption rates are relatively low (Vigg et al. 1991), and northern squawfish swimming ability would presumably be minimal. In addition to creating an area that excludes predators, high flows should also move juvenile fish downstream faster and keep them out of predator inhabited eddies or littoral areas.

During times when river flows are below the maximum prolonged performance of northern squawfish, the energetic benefits and costs of maintaining position and feeding may determine whether they would inhabit areas around bypass outlets. Although Hughes and Dill (1990) challenged the notion that fish maximize their net energy gain by selecting a water velocity that optimizes the tradeoff between food supply and swimming cost (Jenkins 1969; Bachman 1984; Fausch and White 1981; Fausch 1984), this view seems probable in the case of northern squawfish predation. The metabolic costs associated with prolonged speeds and maintaining position increase directly with water velocity and may involve both aerobic and

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anaerobic processes (Beamish 1978; Facey and Grossman 1990). The high energetic demands of a three-staged (approach, chase, and strike) predatory strategy (Harper and Blake 1988), which we believe typifies northern squawfish behavior (Mesa, unpublished data), would also presumably increase directly with water velocity, thereby ˙ making it unlikely that fish would maintain position and feed in areas of high water velocity. However, Godin and Rangeley (1989) found that juvenile Atlantic salmon (Salmo salar) reduced their reaction and attack distances in response to increasing current velocity and thus reduced their energy cost of travel per attack. A similar strategy by northern squawfish may yield an acceptable net energy gain when feeding in high flows. More research is needed to clarify the energetics and feeding behavior of northern squawfish under different prey density and flow regimes.

In summary, the prospect of using water velocity to exclude or limit northern squawfish predation at bypass outlets appears promising, at least during certain times of the year. Although our fatigue curves are incomplete, we estimate that northern squawfish would not be able to maintain position at water velocities above 150 cm/s. We recommend the construction of new or modification of existing bypass facilities include an area of high water velocity around the outlet, provide few eddies and minimal submerged cover, and be located away from littoral areas.

References

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream Transactions of the American Fisheries Society 113:1-32.

Bainbridge, R. 1962. Training, speed, and stamina in trout. Journal of Experimental Biology 39:537-555.

Beamish, F. W H. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. II. Influence of weight and temperature on respiration of several species. Canadian Journal of Zoology 42:177-188.

Beamish, F. W H. 1978. Swimming capacity. p. 101 - 175. In W S. Hoar and 0.3. Randall [ed.] Fish physiology. Academic Press, New York, New York.

Beamesderfer, R. C., R. E. Rieman, J.C. Elliott, A. A. Nigro, and D. L. Ward. 1987. Distribution, abundance and population

dynamics of northern squawfish, walleye, smallmouth bass, and channel catfish in John Day Reservoir, 1986. Annual Progress Report. Bonneville Power Administration, Portland, Oregon.

Beitinger, T. L. and R. W. McCauley. 1990. Whole-animal physiological processes for the assessment of stress in fishes. Journal of Great Lakes Reservoirs 16:542-575.

Bell, W H. and L. D. B. Terhune. 1970. Water tunnel design for fisheries research. Fisheries Research of Canada Technical Report No. 195.

Bennett, A.F., T. Garaland, and P.L. Else. 1989. Individual correlation of morphology, muscle mechanics, and locomotion in a salamander. American Journal of Physiology 256 (Regulatory Integrative Comp. Physiol.) 25:R1200 - R1208.

Bernatchez, L. and J.J. Dodson. 1985. Influence of temperature and current speed on the swimming capacity of lake whitefish (Coreaonus clupeaformis) and cisco (II, artedii). Canadian Journal of Fisheries and Aquatic Sciences 42: 1522-1529.

Berry, C. R. Jr. and R. Pimental. 1985. Swimming performances of three rare Colorado River fishes. Transactions of the American Fisheries Society 114:397-402.

Beyer, J.M, G. Lucchetti, and G. Gray. 1988. Digestive tract evacuation in northern squawfish (Ptychocheilus Oregonensis). Canadian Journal of Fisheries and Aquatic Sciences 45:548-553.

Brett, J.R. 1967. Swimming performance of sockeye salmon (Oncorhynchus nerka) in relation to fatigue time and temperature. Journal of the Fisheries Research Board of Canada 24:1731-1741.

Brett, J.R. and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (Oncorhyncus nerka) in relation to size and temperature. Journal of the Fisheries Research Board of Canada 30:379-387.

Brown, L. R. and P. B. Moyle. 1981. The impact of squawfish on salmonid populations: A review. North American Journal of Fisheries Management 1:104-111.

Collins, G. B., J.R. Gauley, and C. H. Elling. 1962. Ability of salmonids to ascend high fishways. Transactions of the American Fisheries Society 91:1-7.

Davis, G. E., J. Foster, C. E. Warren, and P. Doudoroff. 1963. The influence of oxygen concentration on the swimming performance of juvenile Pacific salmon at various temperatures. Transactions of the American Fisheries Society 92:111-124.

Dorn, P., L. Johnson, and C. Darby. 1979. The swimming performance of nine species of common California inshore fishes. Transactions of American Fisheries Society 108:366-372.

Facey, D. E. and G. D. Grossman. 1990. The metabolic cost of maintaining position for four North American stream fishes: effects of season and velocity. Physiological Zoology 63:757-776.

Faler, M. P., L. M. Millar, and K.I. Welke. 1988. Effects of variation in flow on distributions of northern squawfish in the Columbia River below McNary Dam. North American Journal of Fisheries Management 8:30-35.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441-451.

Fausch, K. D. and R.J. White. 1981. Competition between brook trout (<u>Salvelinus fontinalis</u>) and brown trout (<u>Salmo trutta</u>) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220-1227.

Garland, T. and P. L. Else. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in a lizard. American Journal of Physiology (Regulatory Integrative Comp. Physiol .) 247:R806-R815.

Gleeson, T. T. and J.M. Harrison. 1988. Muscle composition and

its relation to sprint running in the lizard, _Dipsosaurus dorsalis._ American Journal of Physiology (Reg. Int. Comp. Physiol.) 24:R470-R477.

Glova, G. J. and J. E. McInerney. 1977. Critical swimming speeds of coho salmon (Oncorhyncus kisutch) fry to smolt stages in relation to salinity and temperature. Journal of the Fisheries Research Board of Canada 34:151-154.

Goulden, C. H. 1952. Methods of statistical analysis. John Wiley and Sons, Inc. New York, New York.

Godin, J. J. and R. W. Rangeley. 1989. Living in the fast lane: effects of cost of locomotion on foraging behavior in juvenile Atlantic salmon. Animal Behaviour 37:943-954.

Harper, D. G. and R. W Blake. 1988. Energetics of piscivorous predator-prey interactions. Journal of Theoretical Biology 134:59-76.

Hughes, N. F. and L. M Dill. 1990. Position choice by drift-feeding salmonids: model and test for Artic grayling (Thymallus arcticus) in subartic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:2039-2048.

Jenkins, T. M, Jr. 1969. Social structure, position choice and micro-distribution of two trout species (Salmo trutta and Salmo gairdneri) resident in mountain streams. Animal Behaviour Monographs 2:56-123.

Jeppson, P. W and W S. Platts. 1959. Ecology and control of the Columbia squawfish in northern Idaho lakes. Transactions of the American Fisheries Society 88:197-202.

Jones, D. R. , J. W Kiceniuk, and O. S. Bamford. 1974. Evaluation of the swimming performance of several fish species from the Mackenzie River. Journal of the Fisheries Research Board of Canada 31:1641-1647.

Kolok, A. S. In review. Morphological and physiological correlates with swimming performance in juvenile largemouth bass. American Journal of Physiology.

Matthews, G. M, D. L. Park, S. Achord, and T.E. Ruehle. 1986.
Static seawater challenge test to measure relative stress
levels in spring chinook salmon smolts. Transactions of the
American Fisheries Society 115:236-244.

Maule, A. G., C. B. Schreck, C. S. Bradford, and B.A. Barton. 1988.
Physiological effects of collecting and transporting
emigrating juvenile chinook salmon past dams on the Columbia
River. Transactions of the American Fisheries Society
117:245-261.

Moyle, P. B. 1976. Inland fishes of California. University of
California Press. Berkeley, California.

Nigro, A. A., S. Vigg, and C. Burley. 1990. Development of a
system-wide predator control program stepwise
implementation, of a predation index, predator control
fisheries, and evaluation plan in the Columbia River Basin.
Annual Progress Report, August 1988 -September 1989, Project
Summary. Project Number 82-028, Bonneville Power
Administration, Portland, Oregon.

Ott, L. 1977. An introduction to statistical methods and data
analysis. Duxbury Press, North Scituate, Massachusetts.

Petersen, J. H., D. B. Jepsen, R. D. Nelle, R.S. Shively, R.A.
Tabor, and T. P. Poe. 1990. System-wide significance of
predation on juvenile salmonids in Columbia and Snake River
Reserviors. Annual Report of Research, 1990. Bonneville
Power Administration, Portland, Oregon.

Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast.
1991. Feeding of predaceous fishes on out-migrating
juvenile salmonids in John Day Reservoir, Columbia River.
Transactions of the American Fisheries Society 120:405-420.

Ricker, W. E. 1941. The consumption of young sockeye salmon by
predaceous fish. Journal of the Fisheries Research Board of
Canada 5:293-313.

Slatick, E. 1971. Passage of adult salmon and trout through an
inclined pipe. Transactions of the American Fisheries
Society 100:448-455.

Scott, W. B. and E.J. Crossman. 1973. Freshwater fishes of
      Canada.   Bulletin 184.   Fisheries Research Board of Canada,
      Ottawa.

Taylor, E. B. and J.D McPhail. 1985. Variation in burst and ·
      prolonged swimming performance among British Columbia
      populations of coho salmon, Oncorhvnchus kisutch.a d i a n
      Journal of Fisheries and Aquatic Sciences 42:2029-2033.

Taylor, E. B. and C.J. Foote.   1991. Critical swimming velocities
      of juvenile sockeye salmon and kokanee, the anadromous and
      non-anadromous forms of Oncorhvnchus nerka (Walbaum).
      Journal of Fish Biology 38:407-419.

Thomas, A. E., R. E. Burrows, and H. H. Chenoweth. 1964. A device
      for stamina measurement of fingerling salmonids. U. S. Fish
      and Wildlife Service Research Report 67.

Thompson, R. B. and D. F. Tufts. 1967. Predation by Dolly Varden
      and northern squawfish on hatchery-reared sockeye salmon in
      Lake Wenatchee, Washington.   Transactions of the American
      Fisheries Society 96:424-427.

Tsuyuki, H. and N. Williscroft. 1977. Swimming stamina
      differences between genotypically distinct forms of rainbow
      (Salmo gairdneri) and steelhead trout. Journal of the
      Fisheries Research Board of Canada 34:996-1003.

Tyus, H. M 1990.   Potamodromy and reproduction of Colorado
      squawfish in the Green River Basin, Colorado and Utah.
      Transactions of the American Fisheries Society 119:1035-
      1047.

Tyus, H. M, B. D. Burdick, and C. McAda. 1984. Use of
      radiotelemetry for obtaining habitat preferrence data on
      Colorado squawfish.   North American Journal of Fisheries
      Management 4:177-180.

Uremovich, B. L., S. P. Cramer, C. F. Willis, and C.O. Junge. 1980.
      Passage of juvenile salmonids through the ice-trash
      sluiceway and squawfish predation at Bonneville Dam, 1980.
      Oregon Department of Fish and Wildlife, Clackamas, Oregon.

Videler, J.J. and C. S. Wardle. 1991. Fish swimming stride by

stride: speed limits and endurance. Reviews in Fish
Biology and Fisheries 1:23-40.

Vigg, S., T.P. Poe, L.A. Prendergast, and H.C. Hansel. 1991.
Rates of consumption of juvenile salmonids and alternative
prey fish by northern squawfish, walleyes, smallmouth bass,
and channel catfish in John Day Reservoir, Columbia River.
Transactions of the American Fisheries Society 120:421-438.

Vigg, S. and C.C. Burley. 1991. Temperature dependent maximum
daily consumption of juvenile salmonids by northern
squawfish (<u>Ptychocheilug</u> <u>orregonensis</u>) from the Columbia
River. Canadian Journal of Fisheries and Aquatic Sciences
48: 2491-2498.

Walsberg, G.E., M.S. Lea, and S.S. Hillman. 1986. Individual
variation in maximum aerobic capacity: Cardiovascular and
enzymatic correlates in <u>Rena</u> <u>catesbiana</u>. Journal of
Experimental Zoology 239: l-5.

Webb, P.W 1975. Hydrodynamics and energetics of fish
propulsion. Fisheries Research Board of Canada Bulletin
190.

Williams, I.V. and J.R. Brett. 1987. Critical swimming speed of
Fraser and Thompson River pink salmon (<u>Onchorvnchus</u>
<u>gorbuscha</u>). Canadian Journal of Fisheries and Aquatic
Sciences 44:348-356.

Report 6

Reproduction and early life history of northern squawfish
Ptvchocheilus oreaonensis in the Columbia River

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Abstract

Little is known about northern squawfish Ptvchocheilus
oregonensis reproduction and early life history in the Columbia
River. Thus, in 1991 we initiated a small-scale study consisting
primarily of literature searches and preliminary field and
laboratory investigations. Limited sampling was conducted for
northern squawfish eggs and larvae in shallow littoral areas of
the upper Bonneville pool and in the mouth of the Deschutes
River. In the laboratory, northern squawfish larvae were
cultured to obtain a developmental series for identification
purposes. Additionally, data and curated samples collected
during previous ichthyoplankton studies and substrate map
information were examined to locate possible spawning locations
of northern squawfish.

Introduction

Northern squawfish Ptvchocheilus oreaonensis have been
identified as major predators of juvenile salmonids migrating
downstream through Columbia River dams and reservoirs (Poe et al.
1991). Because of this, a variety of northern squawfish removal
programs have been implemented. To effectively manage a fishery,
however, it is necessary to understand all aspects of a fish's
life history. Basic knowledge of reproduction, early life
history, and factors influencing these processes are particularly
important, since the strength of a year-class may be determined
by the survival of egg, larval and juvenile stages.
There is little published information on northern squawfish
reproduction, particularly in the Columbia River system, although
there have been a number of theses, unpublished manuscripts, and

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reports concerning northern squawfish life history. Spawning occurs on sites with rubble-cobble substrates and low water velocities (Jeppson 1957; Jeppson and Platts 1959; Patten and Rodman 1969; Beamesderfer 1983). Spawning depth is variable, ranging from less than 0.3 m in northern Idaho lakes (Jeppson and Platts 1959) to 15 m in the Merwin Reservoir, Washington (Patten and Rodman 1969). Northern squawfish are broadcast spawners with benthic adhesive eggs; Olney (1975) found that in Lake Washington females ranging from 342 to 590 mm total length produced 6,037 to 95,089 eggs. In some localities, spawning aggregations of a few hundred to a few thousand males have been observed (Jeppson 1957; Casey 1962; Patten and Rodman 1969). Females are fewer in number (1F:50-100M). Females swim above or outside the male aggregations and elicit a chase response. Spawning fish have dark lateral bands and males form tubercles on their heads and backs.

Northern squawfish spawning aggregations have not been documented in the Columbia River, and spawning locations are unknown. Vigg et al. (USFWS, unpublished data) examined gonads of northern squawfish captured in the John Day Reservoir on the Columbia River in 1982 and 1986, and reported that spawning occurred in June and July at water temperatures of 15 to 19°C. Distributions of northern squawfish larvae and juveniles have been more fully studied than spawning in this reservoir (Hjort 1981; LaBolle 1984; LaBolle et al. 1985). Larvae of northern squawfish and chiselmouth Acrocheilus alutaceus (which cannot currently be separated) dominated the catch (57.7%) in upper littoral habitats in John Day Reservoir. Greatest abundances of larval northern squawfish occurred in tailrace areas in contrast to lower larval densities in forebay areas.   A diel pattern of abundance was observed, with high densities of larvae in very shallow (< 0.15 m depth) habitats during the day.

There are many unanswered questions concerning the life history of the northern squawfish. In contrast, the Colorado squawfish Ptychocheilus lucius has been more fully studied (Marsh 1985; Nesler et al. 1988; Haines and Tyus 1990; Karp and Tyus 1990; Tyus 1990; Tyus and Haines 1991; McAda and Kaeding 1991; Tyus 1991). Adult Colorado squawfish have been radio-tagged in order to follow spawning migrations and determine spawning sites (Tyus 1990; McAda and Kaeding 1991). Radio-tagging has disadvantages, however, in that it is difficult to verify that tracked movements are spawning-related and to pinpoint the exact time and location (i.e. depth) of spawning. Tyus (1990) found that tagged Colorado squawfish in the Green

River basin of Colorado and Utah migrated to spawning areas an average of 140.7 km both up- and downstream and spawned as summer flows decreased and water temperatures increased. McAda and Kaeding (1991) reported that tagged Colorado squawfish in the upper Colorado River remained dispersed throughout the spawning season instead of forming spawning aggregations and suggested that spawning habitats might be widespread. Researchers have also used larval drift nets to estimate Colorado squawfish spawning times and locations (Nesler et al. 1988; Tyus and Haines 1991). Spawning dates were determined by back-calculating larval age from length based on larval growth in the laboratory.

The goal of the current study is to research various aspects of northern squawfish reproduction and early life history. This information would greatly aid in controlling northern squawfish populations. For example, if northern squawfish form spawning aggregations at specific sites and times, removal programs could focus on these areas. Knowledge of locations with high concentrations of northern squawfish eggs and larvae might result in programs aimed at controlling northern squawfish numbers during these early vulnerable stages. This strategy has been considered previously; Jeppson (1957) recommended lowering Idaho lake levels to dessicate northern squawfish eggs. Additionally, the identification of factors influencing survival of northern squawfish eggs and larvae would aid in predicting year-class strength and thus be a valuable management tool.

In 1991, we conducted literature searches and preliminary small-scale field and laboratory investigations. In the field, we sampled from June through September for northern squawfish eggs and larvae near possible spawning locations and in shallow littoral areas of the upper Bonneville pool and in the mouth of the Deschutes River. One meter plankton nets attached to the shore and a manually towed D-ring net were used. Samples contain various catostomid and cyprinid larvae and juveniles. Samples have not been fully examined, however, and will not be discussed further. In the laboratory, we successfully cultured northern squawfish larvae to obtain a developmental series for identification purposes. Additionally, we analyzed existing data from white sturgeon project ichthyoplankton collections and substrate map information to locate possible spawning locations of northern squawfish. This information will be used to plan future sampling locations.

Methods

Spawning locations.-We examined abundances of cyprinid larvae in samples collected by the U.S. Fish & Wildlife Service during investigations on the early life history of white sturgeon. Samples considered were collected with beam trawls and D-shaped larval nets (mesh sizes = 1.59 mm) from April through July during 1988, 1989, and 1990 in Bonneville and The Dalles pools.

Samples were chosen for general consistency in sampling effort among months, years, and from pool to pool. John Day Pool was not considered because sampling was not begun until 1989 and was initially exploratory; low numbers of cyprinid larvae were collected (a total of 10 in 1989 and 21 in 1990). Samples from August 1988-1990 were not included due to inconsistencies in effort, although the limited sampling that was conducted collected no cyprinid larvae in The Dalles pool and very few in Bonneville Pool.

Potential spawning habitat was identified using cartographic modeling with a geographic information system (GIS). The GIS contains digitized files of substrate types and depth contours of the Columbia River from the mouth to McNary Dam Two depth intervals (0-12' and 12-30') and two substrate types (gravel, 2.0 mm - 64.0 mm, and rubble/cobble, 64.0 mm - 250.0 mm) were considered since spawning habitat has not been conclusively defined for northern squawfish of the Columbia River basin.

Laboratory Culture.-Northern squawfish were collected from the Columbia River by boat electroshocking during June 1991. Males were selected that were running ripe, and females were selected that appeared to have developing ovaries. Fish were held in the laboratory at 14°C in indoor circular tanks (1.5 m diameter, 0.8 m deep). Two days after collection, two females (both 440 mm FL) were injected with lutenizing hormone-releasing hormone analog (LHRH-a) at a dosage of 50 µg/kg of body weight, and two females (460 mm and 520 mm FL) were injected with powdered carp pituitary at 4 mg/kg. Hormones were dissolved in an isotonic sodium chloride solution and injected into the dorsal musculature with 3-cc syringes fitted with 23-gauge needles. Fish were inspected daily for signs of gonad maturation.

Newly-fertilized northern squawfish eggs were placed on 0.3 mm mesh screening in an indoor circular tank (0.6 m diameter, 0.4 m deep) with aerated flow-through well water. Aquarium heaters maintained water temperature at 17°C; temperature was raised to

19-20°C after hatching. A week after hatching, we began feeding larvae newly-hatched brine shrimp _Artemia_ spp. nauplii to excess daily. Larvae were sampled daily and preserved in 5% formalin to obtain a developmental series. Lengths of larvae anesthesized in MS-222 were measured at intervals.

Results and Discussion

Spawning locations There are limitations in using data from the white sturgeon project to study abundances of cyprinid larvae throughout the Columbia River. Because sampling efforts were concentrated in the tailraces of dams we cannot eliminate the possibility of cyprinid larvae occurring in other sections of the river. Tows were conducted for thirty minutes; filtered water volumes may have varied, however, due to fluctuations in discharge levels at the dams.

The highest numbers of cyprinid larvae were collected in a two mile section of the river in Bonneville Pool just downstream from The Dalles Dam (Figure 1) and in a two mile section in The Dalles Pool below John Day Dam (Figure 3). These are also areas with extensive potential spawning sites (Figures 2 and 4). Evaluation of potential northern squawfish spawning habitat throughout the river using the GIS led to the identification of sections with large amounts of suitable habitat. Two such sections occur in The Dalles pool from below Miller Island to John Day Dam (Figure 5) and in the upper half of John Day Pool. Very little potential spawning habitat was identified elsewhere in The Dalles, John Day or Bonneville Pools except directly downstream from The Dalles Dam (Figure 1).

Since the age of larvae at time of collection is unknown it is not possible to estimate precise spawning dates. However, larval abundances suggest that spawning occurred earlier in The Dalles Pool (approximately June) than in Bonneville Pool (approximately July) (Figures 1 and 3).

Laboratory culture.-Two days after hormone injection, viable eggs were easily stripped from all four females and fertilized with three ripe males. Fertilized eggs were negatively buoyant and somewhat adhesive with large yellow or pale orange yolks. At 17°C, developing eggs (mean diameter 2.70 mm, SD 0.12, n = 40) hatched in 7 days. Immediately after hatching, yolk-sac larvae were 7.8 mm notochord length (SD 0.22, n = 8). Larvae remained closely aggregated on the tank bottom for about a week and than swam up into the water column. Larvae were observed to feed on brine shrimp nauplii 9 days after hatching. Larval survival was
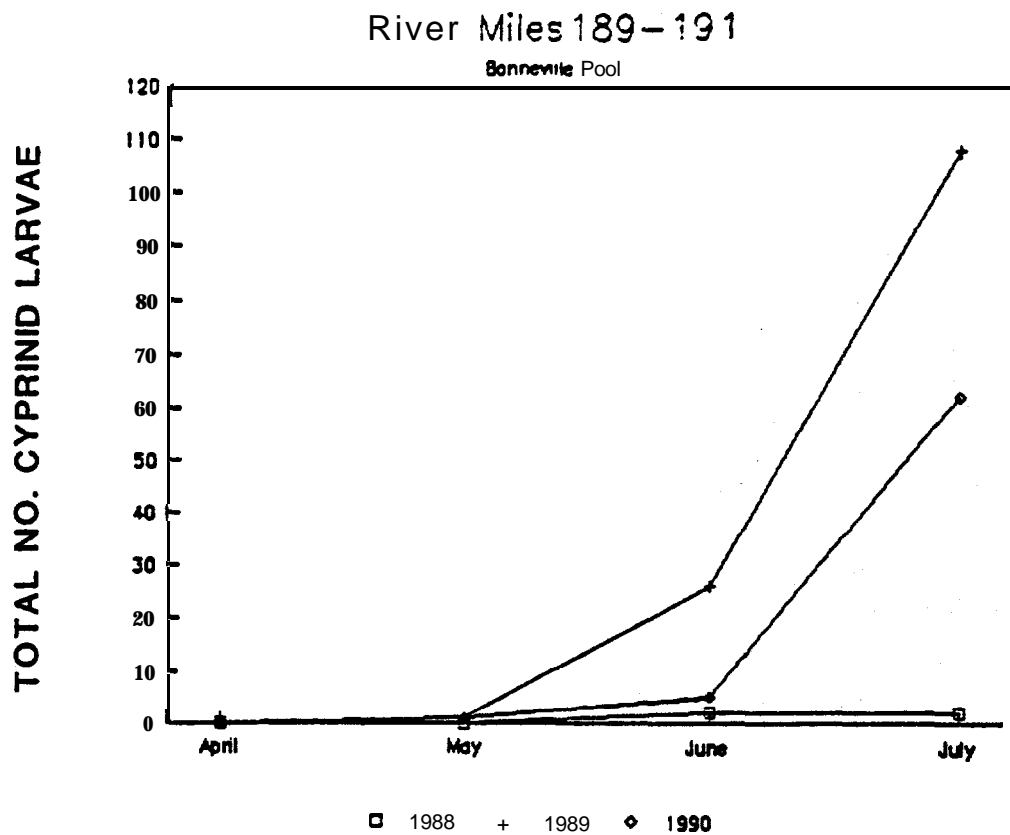
85

Bonneville Pool

TOTAL NO. CYPRINID LARVAE

☐ 1988   + 1989   ◇ **1990**

Figure 1.   Abundances of **cyprinid** larvae in samples **collected** from river miles 189 to 191 in Bonneville Pool.

☐ Gravel &/or Rubble/Cobble Substrate, 8' - 12' Depth
■ Gravel &/or Rubble/Cobble Substrate, 12' - 30' Depth
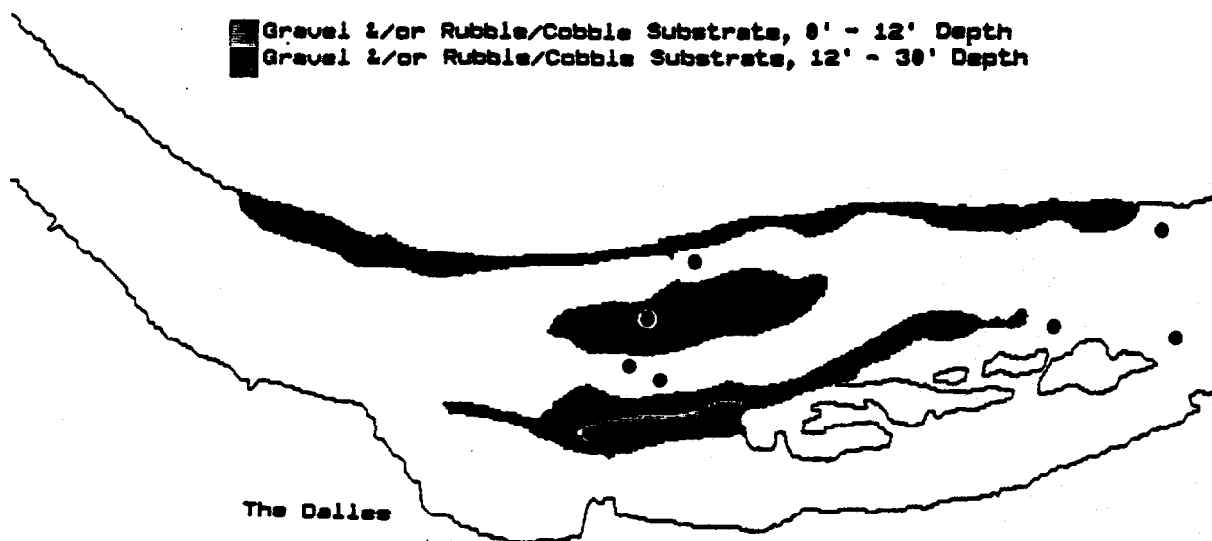
The Dalles

Figure 2.   Potential northern squawfish spawning habitat from river miles 189 to **191 in** Bonneville Pool.   **Dots** mark sampling **locations.**
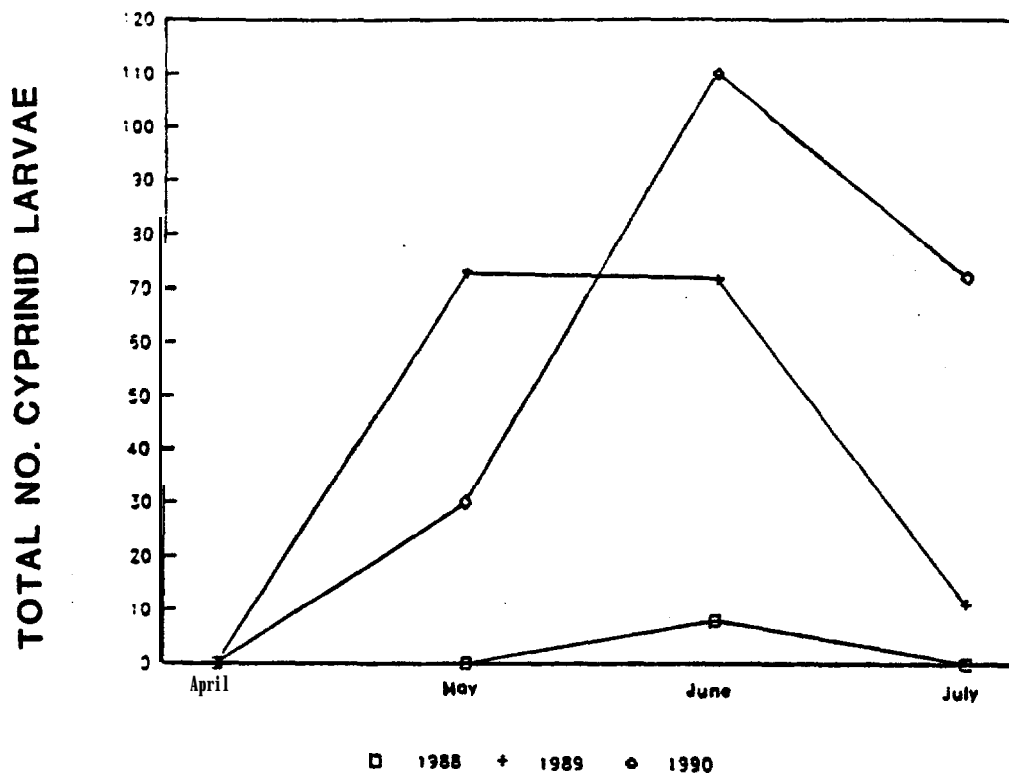
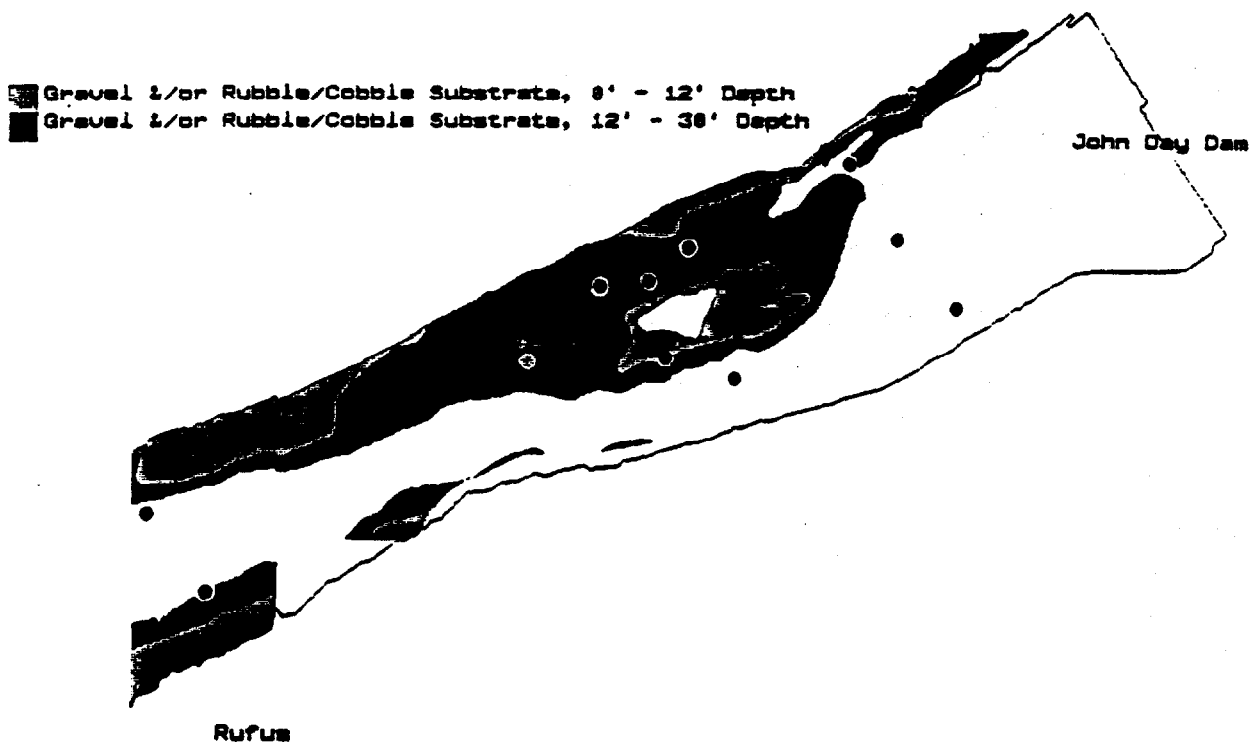Figure 3. Abundances of cyprinid larvae in samples collected from river miles 214 to 216 in The Dalles Pool,

Figure 4. Potential **northern** squawfish **spawning habitat** from river miles 214 to 216 in The **Dalles** Pool. Dots **mark** sampling locations.
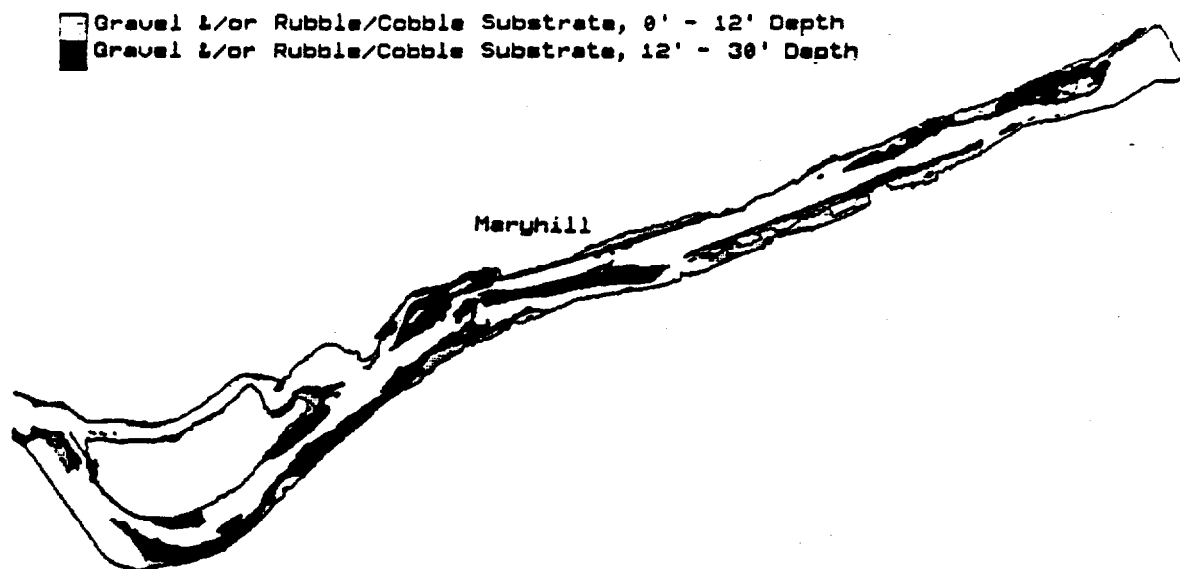
Figure 5.   Potential northern **squawfish spawning habitat in The**
Dalles Pool from river mile 203 to 216.5.

very high, essentially 100%. A month after hatching, mean standard length was 14.2 mm (SD 0.6; n = 20).

Based on laboratory results, the following life history scenario is probable in -the field. Eggs spawned over rubble-cobble substrate remain attached to the benthos for approximately a week until hatching. Newly-hatched larvae remain in interstitial spaces for a week until emergence; they are then under the influence of water currents and are dispersed unknown distances downriver until they aggregate in shallow littoral areas. The timing of these events is dependent upon river temperature since development rate is directly proportional to temperature.

References

Beamesderfer, R. C. 1983. Reproductive biology, early life history, and microhabitat of northern squawfish, (Ptvchocheilus oregonensis) in the St. Joe River, Idaho. Master's Thesis. University of Idaho, Moscow.

Casey, 0. E. 1962. The life history of the northern squawfish in Cascade Reservoir. Master's Thesis. University of Idaho, Moscow.

Haines, G. B., and H. M Tyus. 1990. Fish associations and environmental variables in age-0 Colorado squawfish habitats, Green River, Utah. Journal of Freshwater Ecology 5:427-435.

Hjort, R. C., B. C. Mundy, and P. L. Hulett. 1981. Habitat requirements for resident fishes in the reservoirs of the lower Columbia River. Army Corps of Engineers,, Final Report Contract No. DACW57-79-C-0067.

Jeppson, P. 1957. The control of squawfish by use of dynamite, spot treatment, and reduction of lake levels. The Progressive Fish-Culturist 19:168-171.

Jeppson, P. W, and W S. Platts. 1959. Ecology and control of the Columbia squawfish in northern Idaho lakes. Transactions of the American Fisheries Society 88:197-202.

Karp, C. A., and H. M Tyus. 1990. Behavioral interactions between young Colorado squawfish and six fish species. Copeia 1:25-34.

LaBolle, J., LD. 1984. Importance of the upper littoral zone as
     rearing area for larval and juvenile fishes in a Columbia
     River impoundment. Master's Thesis. Oregon State University,
     Corvallis.

LaBolle, L. D., H. W. Li, and B. C. Mundy. 1985. Comparison of
     two samplers for quantitatively collecting larval fishes in
     upper littoral habitats. Journal of Fish Biology 26:139-146.

Marsh, P. C. 1985. Effect of incubation temperature on survival
     of embryos of native Colorado River fishes. The Southwestern
     Naturalist 30:129-140.

McAda, C. W., and L. R. Kaeding. 1991. Movements of adult
     Colorado squawfish during the spawning season in the upper
     Colorado River. Transactions of the American Fisheries
     Society 120: 339-345.

Nesler, T. P., R. T. Muth, and A. F. Wasowicz. 1988. Evidence
     for baseline flow spikes as spawning cues for Colorado
     squawfish in the Yampa River, Colorado. American Fisheries
     Society Symposium 5:68-79.

Olney, F. E. 1975. Life history and ecology of the northern
     squawfish Ptychocheilus oreaonenesis (Richardson) in Lake
     Washington. Master's Thesis Thesis. University of
     Washington, Seattle.

Patten, B. G. 1960. A high incidence of the hybrid Acrocheilus
     alutaceum X Ptychocheilus oreaonense. Copeia 1:71-73.

Patten, B. G., and D. T. Rodman. 1969. Reproductive behavior of
     northern squawfish, Ptychocheilus oregonenesis. Transactions
     of the American Fisheries Society 198:108-111.

Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A.
     Prendergast. 1991. Feeding of predaceous fishes on
     out-migrating juvenile salmonids in John Day Reservoir,
     Columbia River. Transactions of the American Fisheries
     Society 120:405-420.

Stewart, K. W. 1966. A study of hybridization between two
     species of cyprinid fishes, Acrocheilus alutaceus and

<u>Ptychocheilius</u> <u>oregonensis.</u> PhD Thesis. University of British Columbia, Vancouver.

Tyus, H. M 1990. Potamodromy and reproduction of Colorado squawfish in the Green River Basin, Colorado and Utah. Transactions of the American Fisheries Society 119:1035-1047.

Tyus, H. M 1991. Movements and habitat use of young Colorado squawfish in the Green River, Utah. Journal of Freshwater Ecology 6:43-51.

Tyus, H. M, and G. B. Haines. 1991. Distribution, habitat use, and growth of age-0 Colorado squawfish in the Green River Basin, Colorado and Utah. Transactions of the American Fisheries Society 120:79-89.

Vigg, S., L. A. Prendergast, and W. R. Nelson. Unpub. Mss. Gonad development and spawning of northern squawfish in a mainstem Columbia River Reservoir. USFWS - Columbia River Field Station, Cook, Washington.

Report 7

Effects of light intensity on northern squawfish capture of juvenile salmonids in the laboratory

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Abstract

Northern squawfish Ptvchocheilus oregoniensis were fed
(ad libitum) juvenile salmonids Oncorhynchus spp. using a normal
light cycle and also with increased nighttime light, to simulate
illumination near dams. The capture rate of salmon by northern
squawfish was inversely related to light intensity. Feeding
rates were lowest at high light intensities (20 and 0.2 ft-
candles), intermediate when light was 0.015 ft-candles, and
highest during low light (~0.001 ft-candles) periods. Increasing
the intensity of light during the night caused northern squawfish
to capture significantly fewer salmon. It may be important to
consider these results when evaluating the best times to release
juvenile salmonids from hatcheries, barges, and bypass
facilities.

Introduction

Northern squawfish Pvchocheilus Oreaonensis are major
predators of juvenile Pacific salmonids Oncorhynehus spp.
migrating down the Columbia River (Poe et al. 1991a). Much of
this predation occurs just below dams (Rieman et al. 1991), -and
thus altered dam operations might be a means to reduce predation
mortality on salmon. Light intensity near dams, bypass outlets,
and hatchery release sites might affect predation, although the
influence of light on northern squawfish predation rates is not
well understood.
Several authors have speculated on the visual feeding
ability of northern squawfish (Steigenberger and Larkin 1974;
Eggers et al. 1978; Vigg et al. 1991), but specific information
about the influence of light intensity on feeding rate is not

available.   Vigg et al. (1991) examined stomach contents of northern squawfish caught in John Day Reservoir (Columbia River) and reported that feeding rate peaked during the day; however, feeding was highest during the nighttime and early morning for fish captured in the boat restricted zone (BRZ) below McNary Dam Vigg et al. (1991) attributed the nighttime feeding peak in the BRZ to either artificial lighting at the dam or high passage rates of juvenile salmonids through McNary Dam during darkness - either mechanism might make prey more available to predators during the night.

Our objectives were to examine how light intensity affects feeding rates of northern squawfish during a normal photoperiod and to determine if increasing light intensity at night (simulating dam lighting) influences predation. This is a study in progress;   in the future we plan to examine diel feeding of northern squawfish in other laboratory systems and review field data on diel feeding (Poe et al. 1991b).

Methods

Laboratory experiments were designed to determine the diel feeding rates of northern squawfish when: (1) light intensity followed a "natural" photoperiod (controls), and (2) nighttime light intensity was increased to simulate dam lighting (treatments).   Control (three total) and treatment (two total) experiments were 4 days in duration, except for the final control period, which was only 2 days.   Control periods were alternated with treatment periods to establish whether predators would return to "normal" control feeding patterns following a light treatment.

Light intensities used in experiments were comparable to light intensities measured in the Columbia River (FWS, unpublished data), except for high daytime sunlight, which could not be reproduced in the laboratory.   For control experiments, three light intensities were used to simulate daylight, morning and evening periods with intermediate light intensity, and night darkness.   Morning and evening periods are called "crepuscular" periods for convenience, although we did not attempt to simulate the change in light intensity that occurs during natural crepuscular times.

Each day was divided into six, 4-h sample periods, with constant light intensity during a period.   Daytime light (0800-1600 hours;   ≈20 ft-candles) was provided by a combination of overhead fluorescent and incandescent bulbs. Crepuscular lighting (0400-0800 and 1600-2000 hours; 0.2 ft-candles) was

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provided by eight 100-W incandescent light bulbs pointed upward to produce a diffuse light. During the night period (2000-0400 hours), all lights were off (<0.001 ft-candles). Treatment light intensities were comparable to light levels in the water near McNary Dam (FWS, unpublished data). For treatment 1, daytime and crepuscular periods were the same as for the controls, but during night (2000-0400 hours), lights remained at crepuscular levels (0.2 ft-candles). During treatment 2, daytime light was the same, but the light intensity during crepuscular and night periods (1600-0800 hours) was lower, 0.015 ft-candles. All photometer readings were taken 10 cm below the water's surface.

Northern squawfish used in experiments were captured by boat electrofishing in the Columbia River near Bonneville Dam, and acclimated in the laboratory for 18 d. Replicate experiments were conducted in six, 1400-L circular tanks (1.5 m diameter) with a partially recirculating water system (Lucchetti and Gray 1988). Water temperature was maintained at $17.5\pm0.5°C$. Waste in tanks was removed by siphoning about every second day. Since data were collected throughout the day, waste was siphoned at variable times to minimize cleaning effects on feeding behavior.

Four northern squawfish were stocked in each of the six tanks; multi'ple predators were used in each tank since isolated northern squawfish do not feed well in the laboratory (FWS, unpublished data). Average northern squawfish fork length (FL) was 438 mm (SD 27; n = 24). To reduce handling effects, the same predators were used in all experiments. Northern squawfish were fed a maintenance diet of juvenile chinook salmon O. tshawytscha. Before experiments began, the light cycle was 12 h light: 12 h dark.

Juvenile chinook salmon were also used as prey-for experiments (99.2 mm FL; SD 8.4; n = 50). Salmon were held in outdoor, 1400-L circular tanks with flow-through well water (7-8°C) and fed a maintenance diet of 2.5 mm commercial moist pellets. One to three days prior to being used in an experiment, chinook salmon were transferred to an indoor tank and acclimated to experimental temperatures and light regimes.

To start the experiments, 12 chinook salmon were added to each tank at 0400 on August 5, 1991. At 4-h intervals (0400, 0800, 1200, 1600, 2000, and 2400 hours), salmon remaining in each tank were counted and the tank was restocked to 12 live salmon. The number of prey eaten per tank per 4-h period was calculated as 12 minus the live salmon count. Twelve salmon per tank could be accurately counted by the observer and provided adequate prey to prevent complete depletion by the predators during 4 hours.

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Counts of salmon during the night periods (dark or low light levels) were made using a flashlight so predators and prey were disturbed as little as possible.   Occasionally, dead salmon with pharyngeal teeth marks along their sides were found in a tank. These salmon were counted as "eaten" since they had obviously been captured and regurgitated by northern squawfish (Gadomski and Hall-Griswold, this report). Dead salmon were removed from tanks as soon as noticed.

Results

During control light conditions, northern squawfish captured more salmon during the nocturnal period (Figure 1A). Over three times as many prey were eaten during eight hours of darkness (2000-0400 hours) as were eaten during bright light (0800-1600 hours; Figure 1A).   Feeding rates during the morning crepuscular period (0400-0800 hours) and the first four hours of bright light (0800-1200 hours) were the lowest (Figure 1A). Feeding increased slightly during the afternoon and the evening crepuscular period (1200-2000 hours; Figure 1A).   Comparable feeding rates did not vary among the three control periods, indicating no change in general (control) feeding activity during the 20-day period of experiments.

Increasing the light level during night periods caused a significant decline in the mean number of salmon captured (Figure 1B).   When night light intensity was increased to 0.2 ft-candles (Treatment 1; Figure 1B), about one salmon was eaten per tank during all 4-h periods;   feeding during the night periods (2000-0400 hours) declined about 70% while feeding rates during other parts of the day remained similar to controls. Increasing the night light intensity to 0.015 ft-candles (Treatment 2; Figure 1B) caused a feeding response that was intermediate between the dark control and the brighter Treatment 1. Treatment 2 feeding rates at 2000, 2400, and 0400 hours were 1.4 to 1.8 prey eaten$\cdot$tank$^{-1}\cdot$4 h^{-1} while feeding rates at other times were lower (Figure 1B).   The mean <u>daily</u> feeding rates for treatments with high light (1.3 prey$\cdot$predator$^{-1}\cdot$day^{-1}) versus low light (1.8 prey$\cdot$predator$^{-1}\cdot$day^{-1}) were significantly different (t-test, P<.01).

The nighttime feeding rate of northern squawfish changed immediately when night light was either increased or decreased (Figure 2).   When night light was increased from dark to about 0.2 ft-candles (Treatment 1), the nighttime feeding rate dropped from 2.7 prey$\cdot$tank$^{-1}\cdot$4 h^{-1} on August 8 to 0.9 prey$\cdot$tank$^{-1}\cdot$4 h^{-1} on
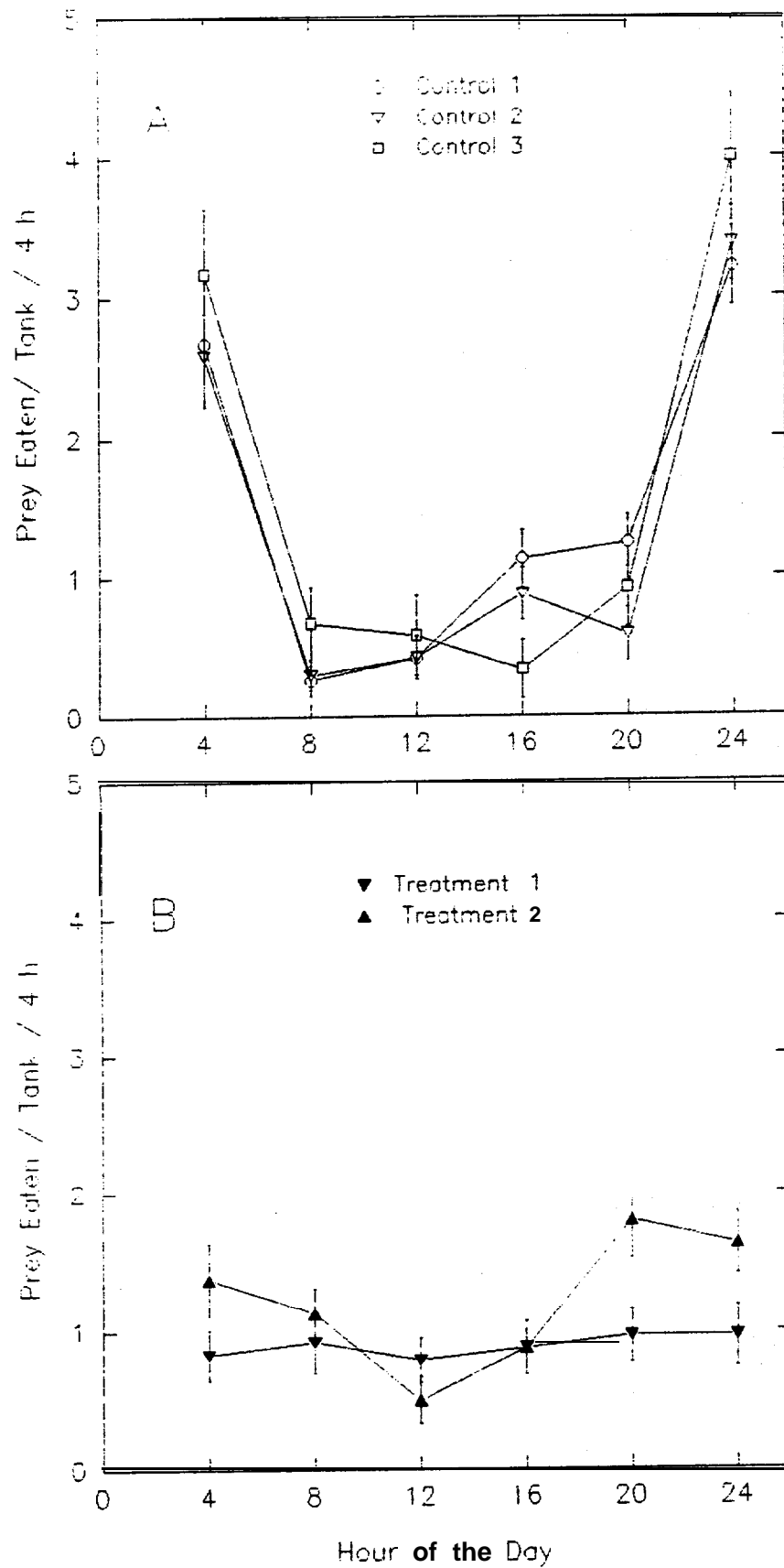
Figure 7. — Mean (SE) number of prey eaten during control (A) and treatment (B) experiments.
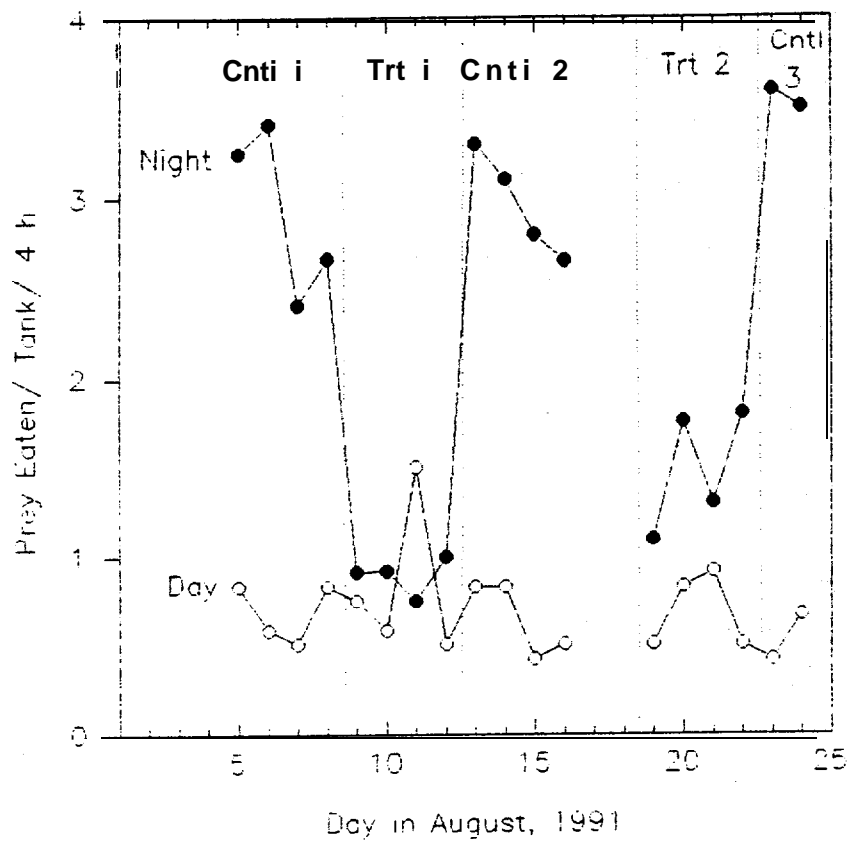
Figure 2. — Mean number of prey eaten during day (0800—1600 hours) and night (2000—0400 hours) periods of all experiments. (Cntl = Control experiment; Trt = Treatment experiment)

August 9.   Data were not collected for two days at the end of the second control period, but it appears that the feeding response was also rapid when night light was increased to 0.015 ft-candles (Treatment 2).   Decreasing the intensity of night light following both treatments, i.e. a return to control conditions, caused the predation rate to immediately increase to the earlier control level (Figure 2).

The general relationship between light intensity and salmon capture rate is shown in Figure 3. At the higher light intensities (both day and crepuscular periods), northern squawfish feeding rate was about constant at 0.7 to 0.8 prey·tank^{-1}·4 h^{-1}.   The capture rate increased linearly with the negative logarithm of light between 10^{-1} and 10^{-3} ft-candles (Figure 3).

During control periods, 25 of 506 salmon eaten (4.9%) were regurgitated, while only one of 303 salmon eaten (0.3%) during treatment periods was regurgitated. The number of salmon regurgitated in a tank was significantly correlated with the total number eaten in that tank (Spearman's rank correlation = 0.12, P=.015 for correlation equal to 0).

Discussion

The capture rate of salmon by northern squawfish was inversely related to light intensity in our experiments.   Feeding rates were lowest during high light intensities (20 and 0.2 ft-candles), intermediate when light was 0.015 ft-candles, and highest during low-light (~0.001 ft-candles) periods (Figure 3). Increasing the intensity of light during the nighttime period caused northern squawfish to capture significantly fewer salmon.

Light has been shown to affect predation in many species of fishes.   Ginetz and Larkin (1976) found that rainbow trout _O. mykiss_ captured more fry of sockeye salmon _O. nerka_ as surface light intensity decreased from 0.30 to <0.01 ft-candles. We measured light at a depth of 10 cm, so the range of light used by Ginetz and Larkin (1976) would roughly compare to our lower light intensities.   Creek chubs _Semotilus atromaaculatus_ were more successful at capturing juvenile blacknose dace _Rhinichthys atratulus_ in tthe dark (0 PA) than in twilight (5 µA) or light (95 µA) conditions (Cerri 1983)   Increased creek chub activity, reduced prey schooling, and-shorter reaction distances by prey were suggested as mechanisms that increased predation during low light periods.   Helfman (1986) characterized cyprinids in general as diurnal feeders, although he notes that exceptions are common

Figure 3. — Mean (SE) number of prey eaten by northern squawfish at four light intensities. Numbers near means are the sample size (number of tanks).
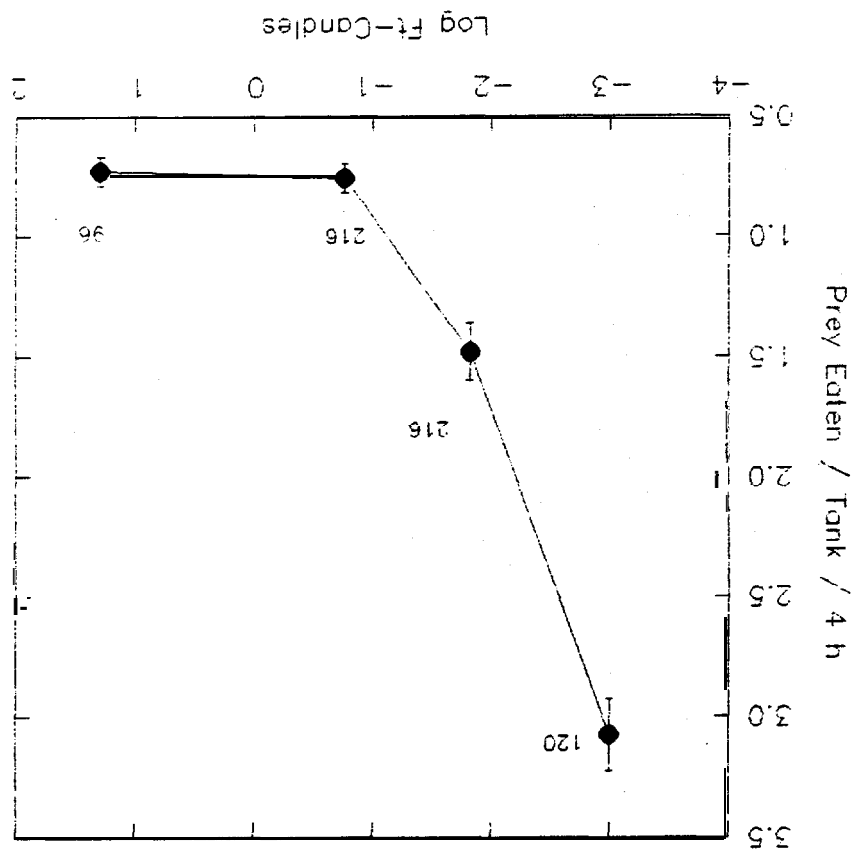
and feeding of predators may be strongly determined by prey activity patterns.

Successful capture of salmon by northern squawfish at very low light intensities may be related to the sensitivity of the predator's eyes, prey vulnerability, or predator activity. Northern squawfish eyes have not been studied, but many teleost eyes are adapted to function at low light intensities (Arnott et al. 1970; Braekevelt 1975; Braekevelt et al. 1989). Walleyes *Stizostedion vitreum vitreum*, for example, develop a reflective material (retinal tapetum lucidum) and bundled macroreceptors in their eyes by the time they reach 140 mm (Braekevelt et al. 1989). These structures increase acuity in dim light and facilitate capture of prey fish in turbid water or low-light environments (Vandenbyllaardt et al. 1991). Many species of prey fish are more vulnerable to predation during darkness due to decreased schooling behavior and a reduction in reaction distance (Whitney 1969; Emery 1973; Vinyard and O'Brien 1976). Juvenile chinook salmon in our experiments appeared to form closer aggregations (schools) during light periods than at night, although this was not quantified. Like some other species (e.g., Cerri 1983), northern squawfish might also become more active during the night, thus encountering and capturing more salmon prey.

Northern squawfish showed a diurnal feeding pattern in John Day reservoir, but feeding rate had two peaks - night and early morning - in the small area just below McNary Dam (Vigg et al. 1991). Northern squawfish feeding was nocturnal in our control experiments, where the light regime should have been roughly comparable to the John Day reservoir light pattern. The difference in feeding pattern between the laboratory and the reservoir could be explained by increased predator activity during daylight in the river, different prey stocks in the field, or differences in prey availability to predators.

Prey availability, or the predator-prey encounter rate, almost certainly differs between our laboratory experiments and natural situations. In our laboratory experiments, salmon were always available to predators since the tanks were relatively small and no refuge was provided for prey. In the river, salmon that are moving or migrating probably have a higher chance of encountering a northern squawfish predator, and thus have a greater probability of being eaten. Juvenile salmon in the lower Columbia River show decreased movements during darkness (Ledgerwood et al. 1991). Juvenile salmonids often pass dams during darkness (Long 1968; Sims et al. 1976; Brege et al. 1988),

which could explain the nocturnal feeding by northern squawfish observed below McNary Dam (Vigg et al. 1991). Spatial segregation of prey from predators in the river could also affect salmon capture rates by northern squawfish. Northern squawfish prefer nearshore, shallow habitats (ODFW and FWS unpublished data), while the distribution of migrating salmonids seems to be stock- and age-specific (e.g., Mains and Smith 1964; Healey 1991; Ledgerwood et al. 1991). Ledgerwood et al. (1991) concluded that subyearling chinook and coho salmon were more likely to be caught nearshore, while yearling chinook salmon, sockeye salmon, and steelhead where usually caught in midriver.

Our experiments suggest changes in night light could be a potential method for reducing predation in localized areas (bypass outlets, hatchery or barge release sites, e.g.). The two treatment light intensities that we tested, 0.2 and 0.015 ft-candles, were within the range of nighttime light intensities encountered near dams; northern squawfish feeding was significantly lower than control feeding at both of the increased light intensities. Increased night lighting near a bypass outlet, for example, might help to reduce the local salmonid mortality. Before recommendations can be firmly made, however, additional studies and analyses should be conducted. We plan (Poe et al. 1991b) to conduct further light experiments in a larger laboratory system (to check for possible tank-size effects) and to re-examine data from past field studies of northern squawfish predation on juvenile salmonids.

References

Arnott, H. J., N. J. Maciolek, and J. A. C. Nicol. 1970. Retinal tapetum lucidum a novel reflecting system in the eye of teleosts. Science. 169:478-480.

Braekevelt, C. R. 1975. Photoreceptor fine structure in the northern pike. Journal of Fisheries Research Board of Canada 32:1711-1721.

Braekevelt, C. R., D. B. McIntyre, and F. J. Ward. 1989. Development of the retinal tapetum lucidum of the walleye (<u>Stizostedion vitreum vitreum</u>). Histology and Histopathology 4:63-70.

Brege, D. A., W. T. Norman, G. A. Swan, and J. G. Williams. 1988. Research at McNary Dam to improve fish guiding efficiency of yearling and subyearling chinook salmon, 1987.

Report to the U.S. Army Corps of Engineers by the National Marine Fisheries Service, Seattle, WA.

Cerri, R. 1983. The effect of light intensity on predator and prey behaviour in cyprinid fish: Factors that influence prey risk. Animal Behavior 31:736-742.

Emery, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. Journal of the Fisheries Research Board of Canada 30:761-774.

Ginetz, R. M, and P. A. Larkin. 1976. Factors affecting rainbow trout (Salmo gairdneri) predation on migrant fry of sockeye salmon (Oncorhynchus nerka). Journal of the Fisheries Research Board of Canada 33: 19-24.

Healey, M 1991. Live history of chinook salmon (Oncorhynchus tshawytscha). Pages 311-394 n C. Groot and L. Margolis, editors. Pacific Salmon Life Histories. UBC Press, Vancouver.

Helfman, G. S. 1986. Fish behavior by day, night and twilight. Pages 366-387 in T. J. Pitcher, editor. The Behavior of Teleost Fishes. The Johns Hopkins University Press, Baltimore.

Ledgerwood, R. D., F. P. Thrower, and E. M Dawley. 1991. Diel sampling of migratory juvenile salmonids in the Columbia River estuary. Fishery Bulletin 89:69-78.

Long, C. 1968. Diel movement and vertical distribution of juvenile anadromous fish in turbine intakes. Fishery Bulletin, U.S. 66:599-609.

Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991a. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day reservoir, Columbia River. Transactions of the American Fisheries Society 120:405-420.

Poe, T. P., 3. H. Petersen, and M G. Mesa. 1991b. Significance of selective predation and development of prey protection measures for juvenile salmonids in Columbia and Snake River reservoirs. Statement of Work to Bonneville Power Administration (BPA Project No. 82-003), Portland, OR.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:448-458.

Sims, C. W, R. C. Johnsen, and W W Bentley. 1976. Effects of power peaking operations on juvenile salmon and steelhead trout migrations, 1975. Final report to U.S. Army Corps of Engineers, National Marine Fisheries Service, Seattle, WA

Vandenbyllaardt, L., F. J. Ward, C. R. Braekevelt, and D. B. McIntyre. 1991. Relationships between turbidity, piscivory, and development of the retina in juvenile walleyes. Transactions of the American Fisheries Society 120:382-390.

Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:421-438.

Vinyard, G. L., and W J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (_Lepomis macrochirus_). Journal of the Fisheries Research Board of Canada 33:2845-2849.

Whitney, R. R. 1969. Schooling of fishes relative to available light. Transactions of the American Fisheries Society 3:497-504.

MAGNITUDE AND **DYNAMICS OF** PREDATION ON **JUVENILE** SALMONIDS
IN **COLUMBIA** AND SNAKE RIVER RESERVOIRS
Annual Report of Research, 1989-1990

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ABSTRACT

    Three aspects of predation upon juvenile salmonids in the
Columbia River are addressed in this report:

    1) Indexina predator consumption. During 1989-90, two
indices of northern squawfish consumption upon juvenile
salmonids were developed for use throughout the Columbia River
Basin. The direct Consumption Index (CI) is based upon the
concept of meal turnover time and takes into account number of
salmonids, temperature, total gut content weight and predator
weight. Computing formulae, laboratory methods, sample size
requirements and preliminary tests are presented. A
Bioenergetics Index (BI) for consumption indexing was also
developed to complement the direct CI. In the BI, growth,
consumption, excretion/evacuation and respiration processes are
modeled to predict the consumption required to produce an
observed growth increment. Preliminary parameter estimates are
presented and a sensitivity study of the model was done to
direct further development.

    2) Studies on predator-smolt dynamics. Northern squawfish
consumption data were collected in the McNary Dam tailrace
during nine days in July, 1988 to improve our understanding of
the predator-smolt functional response. Data were summarized
and fitted, along with July-August data from 1983-86, to a Type
II functional response equation. Maximum consumption
experiments with northern squawfish were completed and results
appear in Appendix A. Finally, a workshop was held to discuss
aspects of predation modeling in the Columbia River. A
separate Bonneville Power Administration report that summarizes
the workshop has been published.

3) <u>Selective **predation** bv northern scuawfish</u>. Laboratory
and field protocols were developed to evaluate northern
sguawfish selection and prey vulnerability. We conducted -
preliminary selection experiments on three categories of
substandard vs. standard juvenile salmonids: live vs. dead;
injured vs. non-injured; and stressed vs. unstressed. Results
from laboratory studies suggest that northern sguawfish prefer
dead over live prey and that descaled prey may be more
vulnerable to predation than non-descaled prey. Stressed and
unstressed prey were consumed in equal proportions when
predation occurred for 6 or 24 h. Physiological and behavioral
effects of stress on juvenile salmon are presented.

BACKGROUND

One of the measures contained in the Northwest Power Planning Council's 1982 Fish and Wildlife Program (Anonymous 1987) called for studies **.....** to investigate juvenile salmon and steelhead losses to predators while these fish are migrating through Columbia and Snake River reservoirs." In response to that measure the Oregon Department of Fish and Wildlife (ODFW) and the U.S. Fish and Wildlife Service (FWS), funded by Bonneville Power Administration (BPA), began a cooperative study in 1982 to estimate the number of juvenile salmonids lost to fish predators in John Day Reservoir. Results of the 1983-86 study indicated that fish predation may account for the majority of unexplained losses **of** juvenile salmonids in John Day Reservoir (Poe and Rieman 1988; Rieman et al. 1988).

Important questions remain to be answered, however, to estimate the system-wide impact of predators on the survival of outmigrating smolts and to determine if predation control is warranted. Although smolt losses to predators were significant in John Day Reservoir, questions remain about the intensity of predation in other Columbia and Snake River reservoirs, cumulative impacts of predators on smolt survival throughout the river system and differential predation-related mortality of healthy versus unhealthy smolts. These questions require a better understanding of predator-prey dynamics at the individual interaction level and at the system level. This project was designed to provide some information on these outstanding questions.

Due to the diverse research objectives in the 1989-90 period, this report is organized into three sections. Section I documents the development of a consumption index, which will be used in conjunction with a predator abundance index (Nigro et al. **1990),** to compare the magnitude of predation in reservoirs throughout the Columbia River Basin. Section II describes the development, testing, and refinement of predation

models. Section III documents the development of protocols to determine if predators select dead, physically injured, or stressed juvenile salmonids as opposed to healthy juvenile salmonids.

SECTION I. PREDATION INDEX

To address the question of system-wide significance of predation, the FWS and ODFW (Poe and Rieman 1988) recommended development of a predation index to estimate the relative magnitude of smolt losses to predators in reservoirs throughout the Columbia River Basin. The index would consist of a Consumption Index, to be developed by FWS, and a Population Abundance Index, to be developed by ODFW. Combination of these indices for an area would yield a Predation Index, similar to a loss estimate. Comparison of Predation Index values among reservoirs would help predict system-wide predation impacts and provide information for directing future predation management decisions.

The FWS objectives were to develop analytical, field and laboratory techniques for a consumption rate index for northern sguawfish (Ptvchocheilus oresonensis), the major fish predator on juvenile salmonids in John Day Reservoir (Rieman et al. 1988). ODFW was to develop corresponding methods for abundance indexing of northern sguawfish. After considering numerous approaches for indexing the juvenile salmonid consumption by northern sguawfish, two methods were selected for development - a direct, limited sampling method [Direct Consumption Index - CI] supplemented by an indirect method based upon predator growth and fish bioenergetics [Bioenergetics Index - BI]. Each method has advantages and disadvantages that will be discussed below. The two methods would act as checks upon each other and should adequately describe predator consumption at sampling locations. The remainder of this section discusses derivation of consumption indices, data requirements, sampling

requirements and pros and cons of the different methods.

Direct Consumption Index (CI)

<u>Backaround</u>

Many methods exist for estimating consumption in fishes
(e.g., Bajkov 1935; Swenson and Smith 1973: Elliott and Persson
1978; Eggers 1979; Pennington 1985; Olsen and Mullen 1986:
Sainsbury 1986) with little agreement upon the **"best"** technique
(Amundsen and Klemetsen 1986: Boisclair and Leggett 1988).
Earlier predation studies in John Day Reservoir used a
modification of the Swenson and Smith (1973) technique to
calculate consumption of juvenile salmonids by resident
predators (Vigg et al. 1988). The modified Swenson and Smith
method combines field diet data and laboratory evacuation
studies to estimate consumption rates. The method can produce
fine-scale temporal estimates of consumption patterns and has
been well developed for the existing predator-prey database.
Disadvantages of this method are its need for extensive diet
data, complex equations with many variables, and the lack of a
variance estimate since consumption is calculated only for the
"typical" predator in the sample.

Consumption was also calculated for predators in John Day
Reservoir by a meal turnover-time method (Rieman et al. 1988)
whose main advantages were variance estimation and simplicity.
This method integrates meal turnover-time and the number of
salmonids found in the gut to calculate consumption for each
individual predator (Henchman 1986; Rieman et al. 1988).

Our consumption index is based upon the concept and simple
equations of meal turnover-time. Modifications of the basic
turnover-time equations were derived and indices computed for
the 1983-86 data set. Index values were correlated with
corresponding consumption estimates computed with the modified
Swenson and Smith method of Vigg et al. (1988). Indices having
the highest correlations with the consumption estimates were

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chosen for further study. We assumed that the modified Swenson and Smith method was the **"best"** estimate of consumption for the John Day predator-prey data set. Consumption indices and methods were tested during the 1989 field **season.** Field and · laboratory methods were developed during 1989 to minimize the time and cost of estimating an index.

Index Derivation

The estimated number of salmonids consumed per day by an individual predator, p, can be expressed as:

$$C_p = \sum_{i=1}^{n} 1 / (\text{Evacuation time for prey item } i)$$

or,

$$C_p = \sum_{i=1}^{n} 1 / D90_i \qquad (1)$$

where C_p is consumption rate (number of salmonids · individual northern squawfish^{-1} · day-'), $D90_i$ is number of days to 90% digestion for salmonid prey item **i**, and n is total number of salmonids found in the gut. Using 90% digestion time, rather than 100%, avoids the problem of non-digestible prey parts that may remain in the gut for extended periods. Equation (1) is equivalent to:

$$C_p = \sum_{i=1}^{n} (24 / T90_i) \qquad (2)$$

where $T90_i$ is number of hours to 90% digestion for the ith salmonid prey item. $T90_i$ was calculated by Beyer et al. (1988) and modified by Rieman et al. (1988) to:

$$T90_i = 1147 * M_i^{0.61} * T^{-1.60} * W_p^{-0.27} \qquad (3)$$

where M_i is meal size (g) at time of ingestion of salmonid prey

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item i, T is water temperature (°C), and W_p is predator weight
(g). Substituting equation 3 into 2 and rearranging gives:

$$C_p = 0.0209 * T^{1.60} * W_p^{0.27} * \sum_{i=1}^{n} M_i^{-0.61} \quad (4).$$

Equation 4 provides an estimate of daily **salmonid** consumption
per northern **squawfish,** but still requires estimation of meal
size (M_i) through intensive gut analysis and complicated data
analysis. Equation 4 was, however, used as a starting point to
derive a series of test formulae (**"indices"**).

Several modifications of equation (4) were examined, trying
different terms for estimating meal size or excluding some
terms. The following formula was chosen as a consumption index
(CI), based upon simplicity of data required and percent
variance explained:

$$CI = 0.0209 * T^{1.60} * MW^{0.27} * [MTsal * MGutwgt^{-0.61}] \quad (5)$$

where T is water temperature, MW is mean predator weight (g),
MTsal is mean number of salmonids per predator, and MGutwgt is
mean gut weight (g) per predator. All variables in CI are
averaged over all predators in a sample; **CI** is the consumption
index for a collection (sample) of predators. Variance of a CI
can be computed by a bootstrap resampling technique (Efron and
Tibshirani 1986).

CI was well correlated with the Swenson and Smith estimates
of consumption for the John Day pool (**r=0.89; P < .001; n=51)**
and the **McNary** Boat Restricted Zone (**r=0.95; P < .001; n=51).**
Calculation of actual consumption (prey-predator-"day-'), rather
than index units, is possible by using the regression equation
shown in Figure 1.

One of the goals of deriving a useful index formula was to
include only variables that could be easily measured in the
field or in the laboratory; index variables whose measurement
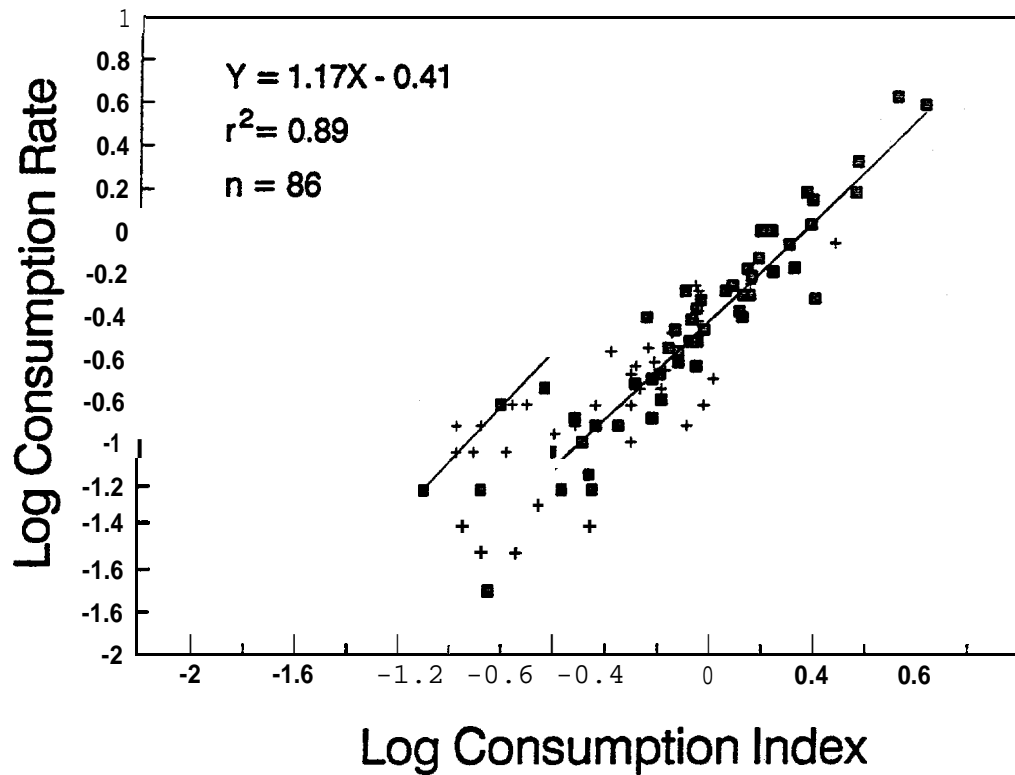
Figure 1. Regression of actual consumption estimates predicted by Consumption Index for McNary BRZ and John Day pool (1983-86). Only days with 15 or more northern squawfish, greater than 250 mm, were used. Squares represent the McNary BRZ (n=51) and crosses represent the John Day pool (n=35); days with a consumption rate of zero were excluded from the regression.

was costly, time consuming or imprecise would defeat the purpose of an index. The only variables needed to calculate CI are predator weight (W), water temperature (T), number of salmonids in the gut (Tsal) and weight of gut contents **(Gutwgt).** Efficient methods for collecting required data have been developed and are described below.

Methods

Field methods were developed and tested during 1989. Northern sguawfish were sampled at 16 stations associated with four different dams (Bonneville, The Dalles, **McNary,** and Ice Harbor). Most effort was centered on **forebay** locations and tailraces, with some sampling in mid-reservoir areas. Predators were collected with an 18 ft, aluminum sled boat equipped with a Smith-Root Type **VIa electrofishing** unit. Pulsed DC (60 and 120 **pulses/sec)** at 700-800 V, drawing 5-6 amps. Electroshocking procedures were similar to those used by Poe et al. (1988) and Vigg et al. (1988).

After capture, northern sguawfish were held in an aerated **livewell** and later placed in water with a lethal dose of ethyl p-aminobenzoate (benzocaine). No stress-induced regurgitation was observed. Predators were measured to the nearest mm (FL), weighed to the nearest 10 g, and scales were collected for age determination. Scales were removed half-way between the posterior base of the dorsal fin and the lateral line. The body cavity of northern sguawfish $\geq$ 250 mm was cut open with a knife, and sex and stage of maturity were determined.

After opening the body cavity, the esophagus was checked for food items. Next, the anterior end of the esophagus was pinched shut and cut behind the pharyngeal teeth. The gut was then extended while fat and viscera were removed from the outer gut wall. The anterior, open end of the gut was next placed into a plastic bag. The **hindgut** was pinched shut near the anus, and, using the thumb and forefinger of the other hand,

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gut contents were squeezed into the plastic bag. The foregut was stripped first to prevent large or sharp food items (such as crayfish exoskeleton fragments and prey fish bones) from lodging. Gut contents were labeled, sealed, and frozen. Potential error in field stripping of northern squawfish guts was evaluated by examining a sub-sample of stripped guts for residual food items with a dissecting microscope. Guts of 38 northern squawfish were stripped and also dissected to determine stripping efficiency.

In the laboratory, gut contents were thawed and weighed to the nearest 0.1 g; an empty bag with label was tared to obtain the actual gut content weight. A digestive enzyme technique was developed and tested to speed processing of gut samples. A digestive enzyme solution was prepared using lukewarm tap water, 2% **w/w** high-strength (8x) porcine **pancreatin,** and 1% **w/w** nonahydrate sodium sulfide (Anderson 1965; Dr. Carl Bond, personal communication). The solution was poured into the plastic sample bags until all gut contents were submersed. The bags were sealed and contents were mixed to insure all food was in contact with the solution. Samples were placed in a **40°C** desiccating oven for about 24 hr. After all flesh was digested, the contents were poured through a **#40** (425 micron) sieve and rinsed with tap water.

Pancreatin digests protein, carbohydrates, lipids, and nucleotides, but not bones, shells, **chitin** or plant cellulose. Diagnostic bones of prey fish were not affected by enzymatic digestion and were enumerated and identified (Hansel et al. 1988). Other major prey groups (mollusks, crustaceans, insects, and plants) were also identified from undigested hard parts. A magnifying glass and dissecting forceps were used to separate diagnostic bones (primarily cleithra, dentaries, opercles, and hypurals) from other bones. Diagnostic bones were examined under a dissecting microscope, keyed to the lowest possible **taxon,** paired to enumerate prey fish consumed and preserved in labeled vials with 95% ethanol.

Sample size analyses were performed to demonstrate the relative efficiency **of** index estimates and to ensure that future efforts would be adequate to accurately evaluate predation intensity. Two components of indexing daily consumption were considered: 1) How many predators must be captured per day to provide an estimate of daily consumption? and 2) How many sampling days are necessary to estimate consumption during a period of time? Data from the 1983-86 Predator-Prey study in John Day Reservoir (Poe and Rieman, 1988) were used in the following analyses.

The effect of the numbers of predators collected upon consumption index (CI) variation was examined using a **"bootstrap"** resampling method. Bootstrap resampling is a nonparametric technique whose only major assumption is that the original sample is representative of the underlying parameter distribution (Efron 1982; Efron and Tibshirani 1986). Sample size was studied by changing the number of predators selected for each bootstrap sample, generating a CI frequency distribution and examining distribution parameters. Boisclair and Leggett (1988) recently used a similar technique for estimating variation of daily fish ration.

In the following discussion, **"sample"** will refer to the total number of predators collected and processed during a time period and **"resample"** will be a randomly selected subset of a sample; a resample may have less than or **equal** to the number of predators in the sample from which it is drawn.

The data were partitioned into four sets: early (May) and late (July) outmigration periods for the pool and the **McNary** Boat Restricted Zone (BRZ). Stratification in this manner was similar to previous work (Vigg 1988; Vigg et al. 1988) and gave adequate samples from which to draw bootstrap resamples. Bootstrap resamples of northern **squawfish** records were generated by randomly selecting, with replacement, records from a data set. For each data set, 250 bootstrap resamples were generated for resample sizes of 5, 15, 30 and 60

predators. Preliminary work indicated that means, coefficients of variation and confidence limits stabilized by taking 250 or more resamples. Resample sizes were chosen since the consumption index was derived from a data set where at least 1-5 fish per day had been collected and more than 60 fish is difficult to process in one day by a two-person crew. For each resample, a CI was calculated. Percentiles (10th and 90th) of the four CI distributions were plotted and examined; minimum sample size was the point along the plot where increasing sample size did not greatly tighten the confidence bounds.

To estimate the number of sample days, daily consumption indices (CI) were computed for Pool and BRZ areas in John Day Reservoir for the early (April-May) and the late (June-August) **smolt** migratory periods. Data were pooled over years and months to increase sample size and for other reasons given in Vigg et al. (1988). CI distributions were not significantly different from normal (Kolmogorov-Smirnov tests) so **sample-**size calculations were based upon the normal distribution. To facilitate comparisons between strata, data were centered to have a mean of 1 by:

$$\text{Standardized } CI_i = CI_i \, / \, \text{Mean } (CI_i),$$

where CI_i was the consumption index on day i. Power curves were computed using a Type I error (Alpha) = **.1** and fixed sample sizes of 2, 4 and 8 days.

Results

Fishing effort for the two-person crew (operator and netter) ranged from 7 to 130 minutes per station. Mean number of salmonids per northern **squawfish** gut was as high as 5.0 (Table 1). Consumption indices (CI) were highest in July in the **McNary** Dam tailrace, an area that has been shown to have a high predation rate (Vigg et al., **1988).** Although sampling was

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not designed for rigorous comparison, CI values were generally.
lower in May than in July (Table 1).

Of the 38 northern squawfish guts that were stripped to
determine stripping efficiency, only four contained prey fish ·
and three of these had residual food items. Food residue,
however, average only 0.03% of weight of original gut contents.
Of the 34 examined stomachs without preyfish, eight had
residual food items (average 0.16% of original gut contents).
Most residual food items were sharp crayfish exoskeleton
fragments, sharp **preyfish** bones such as ribs, vertebrae, etc.,
and minute amounts of plant material. Although few of the
examined predators contained preyfish, careful gut stripping
removed over 99% of the total gut contents by weight and all
diagnostic **salmonid** bones.

The digestive enzyme method tested greatly reduced the cost
and effort required for the laboratory component of the
predation index. The gut analysis technique was approximately
six times faster (person-hrs) than the analysis method used to
process the 1988 samples (see Section II of this report). The
digestive enzyme approach yielded less information, but was
more cost-effective than traditional methods used to estimate
absolute rates of consumption (e.g., Swenson and Smith 1973).

Increasing the number of predators **"sampled"** by
bootstrapping reduced confidence limits of the consumption
index (CI), as expected (Figure 2). In May in the Boat
Restricted Zone (BRZ), confidence limits were fairly close to
the mean and nearly constant for sample sizes of 15 to 60
predators (Figure 2). During July in the BRZ, the mean
consumption index was higher but the pattern of change in
confidence limits was similar to May. A daily sample minimum
of 15 northern squawfish appears sufficient for estimating a
consumption index within boat restricted zones. Larger sample
sizes do not greatly tighten the confidence interval.

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Table 1. Summary of test data from 1989 for northern **squawfish** consumption index. Consumption Index (CI) was calculated only when sample size (N) of northern squawfish was greater than one. `

| 1989 Date	Sample Location	N	Temp. (^{o}C)	Mean			CI
				SQF Wt (g)	Gut Wt (g)	No. of Salm.	
May 12	Bonneville, mid-reservoir	6	12	527	3.7	0.00	**0.00**
May 12	Bonneville, mid-reservoir	10	12	894	13.4	0.00	**0.00**
May 16	The Dalles, mid-reservoir	10	13	1029	14.7	0.10	0.16
May 16	The Dalles, mid-reservoir	13	13	949	7.3	0.00	0.00
May 19	The Dalles, **forebay**	15	13	897	19.1	0.27	0.35
Jul 07	Ice Harbor, **tailrace**	45	17	660	4.8	0.04	0.17
Jul 12	McNary, **tailrace**	23	18	540	7.1	0.87	3.06
Jul 12	McNary, **tailrace**	77	18	574	8.9	1.29	4.02
Jul 13	McNary, **tailrace**	25	19	720	7.0	1.52	6.36
Jul 13	McNary, **tailrace**	4	19	1037	23.2	5.00	11.14
Jul 27	Bonneville I, **tailrace**	23	20	687	2.1	0.13	1.22
Jul 27	Bonneville I, **tailrace**	19	20	803	6.1	0.63	3.22
Jul 28	Bonneville II, **tailrace**	3	19	640	0.5	**0.00**	0.00
Jul 31	Bonneville I, **tailrace**	18	20	800	2.6	0.22	1.87
Jul 31	Bonneville I, **tailrace**	20	20	627	3.0	0.25	1.85
Aug 01	Bonneville II, **tailrace**	10	20	764	2.9	0.00	0.00

McNary Boat Restricted Zone
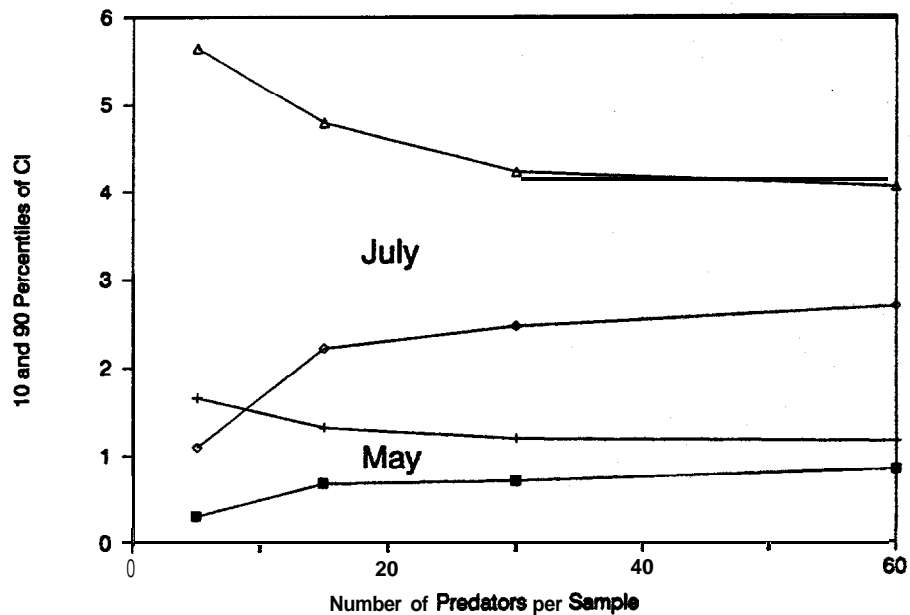
John Day Pool
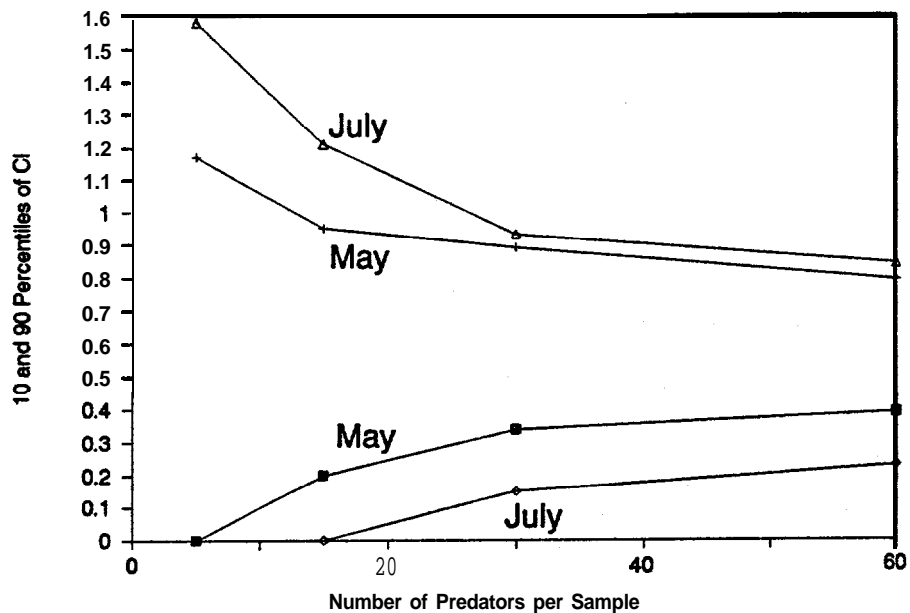
Figure 2. Effect of sample size upon the 10th and 90th percentiles
of bootstrapped consumption index distributions. Each
distribution had 250 computed consumption indices. The number
of original sample days and total predators (days, predators)
per strata were BEE-July (9,589), BEE-May (12,424), Pool-July (6,243)
and Pool-May (15,586).

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Slightly larger sample sizes appear necessary for estimating a consumption index within a reservoir pool (Figure 2). Confidence limits did not stabilize for John Day Pool CI distributions until about 30 predators had been sampled. Consumption indexing during the summer period would require the greatest sampling effort. The central 80% confidence interval for July in the pool ranged from 0 to 1.2 index units when 15 fish were sampled (Figure 2); this interval was reduced to 0.15 to 0.9 index units when sample size was increased to 30 predators.

Increasing the number of sample days in an area (Figure 3) increased the probability that two CI samples (called **"test"** and **"control"** below for convenience) could be distinguished. With 2 days of spring sampling in the BRZ (Figure **3a),** test samples of CI that are two times control or one tenth of control would be detected with about 70% confidence. During the June-August period, samples of 2 days in the BRZ would have low power to distinguish cases when test means were less than twice the control mean (Figure 3b). When test means were triple the control mean, or greater, the probability of falsely rejecting the null hypothesis became very slim in the BRZ (Figure 3b).

Variation of **CI's** in the pool during April-May were comparable to variation in the BRZ (Table **2),** suggesting sampling power would be similar to that described above (see Figures **3a-c).** During summer months, however, day-to-day variability increased and the power of a **2-day** sampling plan thus declines (Figure 3d). Test samples would need to be about three times control samples to have a reasonably high confidence of successful distinction. Sampling on a **4-** or **8-** day schedule increased statistical power and could be used in specific CI comparisons.

BRZ April-May

BRZ June-August

Pool April-May

Pool June-August

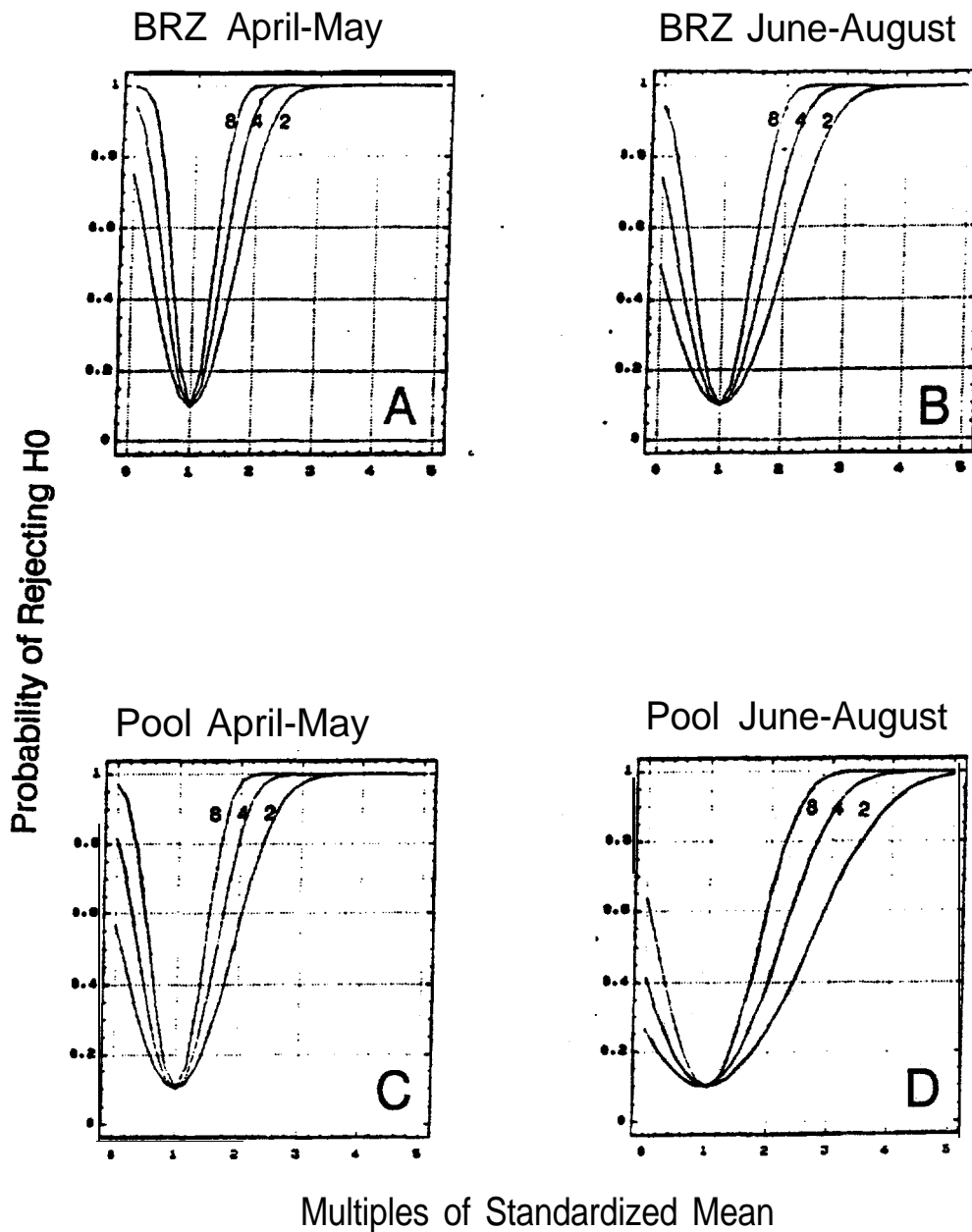**Probability of Rejecting H0**

Multiples of Standardized Mean

Figure 3.   Power of samples of 2, 4 and 8 days of sampling to
distinguish test means from a control mean standardized to
equal one.   The y-axis is the probability of rejecting the null
hypothesis when test and control means differ by some multiple
on the x-axis.   Type I error (alpha) was set to .1 and a two-
tailed test was specified.

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Table 2.   Mean Consumption, Index for time and location strata used in power analyses for number of days.

Location	Time	Number of Sample Days	Mean Consumption Index	Coefficient of Variation (SD / Mean)
JD Pool	Apr-May	20	0.43	0.78
JD Pool	Jun-Aug	31	0.42	1.41
BRZ	Apr-May	20	0.70	0.61
BRZ	Jun-aug	31	1.31	0.87

Discussion

Consumption index sampling in 1989 was done primarily to develop methods, test field procedures and resolve problems. Indices measured during 1989 should be considered test data since sampling criteria were not fully developed, geographic location of samples was not systematic and sample timing was not balanced. The consumption indices were, however, highly variable between sample sites suggesting predation intensity may be variable and **"hot spots"** may be detected with systematic sampling.

The intent in developing the consumption index was to minimize the time and costs associated with sampling the many large reservoirs throughout the Lower Snake and Columbia Rivers. The two components of implementing a system-wide northern squawfish consumption index include the field work required to collect predators and the laboratory work required to process and analyze the **gut** contents. Both field and laboratory methods were modified in an attempt to reduce the costs associated with traditional food habits studies.

The field collection cost during 1989 predation index testing was roughly the same as past field work conducted in

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John Day Reservoir (Poe et al. **1988),** since the costs
associated with hiring personnel, and procurement and
maintenance of vehicles and an **electrofishing boat** are fixed.
Actual field methods using the gut stripping technique required
the same amount of time (-2 minutes per predator) as previous
food habits methods, thus the only alternative to reduce costs
was to reduce sampling effort.

During the 1983-86 predation studies, northern sguawfish
were collected on at least three consecutive days per month,
each day stratified into 6-hour sampling periods (Poe et al.
1988); no specific number of fish was targeted for collection
during a sampling period. During 219 total days sampled, the
median number of northern sguawfish $(\geq$ 250 mm FL) collected and
processed per day was 12 (range l-109 predators). Plans for
consumption indexing throughout the Columbia River system
involves one year's sampling per reservoir, two days in spring
and summer and 15-30 fish per day. Therefore, sampling effort
will be reduced from the 1983-86 effort by collecting fish on
fewer days per year and during a single year: roughly the same
number of fish per sample day will be collected. Also, fewer
sites will be sampled, emphasizing **"hot spot"** areas where'
predation losses are believed to **be** high (i.e., tailraces and
forebays of dams). An index approach requires less effort
since sampling can be less representative than that required
for absolute reservoir-wide estimates of mortality.

Selecting appropriate sample sizes requires some **a** priori
definition of the acceptable error levels, which is not usually
a straight forward task. The analyses above were meant to
describe the confidence in estimating **CI's** that can be expected
with different levels of effort and different sampling
scenarios. The general conclusions were that: 1) samples of
about **15-30** northern sguawfish will be adequate for estimating
daily **CI's,** and, 2) sampling on 2 days will provide a
moderately good estimate of the index of consumption for the
locations and times studied. Daily variability of **CI's** within

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the pool of John Day Reservoir were high during 1983-86, causing **2-day** samples to have only moderate power in distinguishing test from control values. Application of these conclusions to sampling in other reservoirs assumes, of course, that variability will be similar.

Bioenergetic Consumption Index (BI)

Background

Bioenergetics models have become useful tools for studying various aspects of fish growth and consumption (references in Hewett and Johnson 1987; Hewett 1989). Theoretical, laboratory and field studies of fish physiology have been integrated into flexible models, allowing researchers or fisheries managers to estimate consumption or growth of fish from easily measured field data. One approach to indexing consumption in reservoirs throughout the Columbia River system is to develop a bioenergetics model for northern squawfish and use the model to calculate juvenile **salmonid** consumption at study sites based upon observed predator growth and water temperature.

A major advantage of bioenergetic indexing is that it uses fish growth to integrate consumption over a period of time, reducing potential sampling problems associated with variable consumption rates. Juvenile **salmonid** consumption rates are highly variable from day to day, differing by as much as an order of magnitude between successive days (FWS unpublished analyses). Sampling variable consumption patterns with relatively short sample intervals (2-4 successive days) may produce biased estimates if sample dates have particularly low or high consumption. Predators, however, feed throughout the seaward migration period of juvenile salmonids and their growth reflects an integration of daily consumption. Measuring growth rate of predators during the time when juvenile salmonids are passing through a particular reservoir allows estimation of an average daily consumption rate and total consumption for the period.

Two disadvantages of consumption indexing via **bioener-**getics are no immediate, real-time estimates and no specific model has been developed for northern squawfish. Consumption estimates for a time period of interest cannot be made until

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predator growth data have been analyzed at the end of the period. Lack of model development for northern squawfish can be quickly overcome and the remainder of this section describes preliminary development and application of a northern squawfish bioenergetics model. Our general approach is to develop a preliminary model, conduct some test runs of the model, and perform sensitivity analyses upon model parameters. Further development and/or analyses will be recommended based upon results of these test runs and parameter sensitivities.

Model Development

Hewett and Johnson (1987, 1989) developed a generalized bioenergetics model that contains options for selecting equation forms, changing parameters, output formats, etc. Hewett and Johnson's menu-driven program for microcomputers greatly simplifies model development for new species and was used to begin development of the northern squawfish model. Details of model implementation, data files and program options are not provided here, but are available in Hewett and Johnson (1987).

Fish growth may be described or modeled by a simple energy balance equation:

Growth = Consumption - (Respiration + Waste Losses) .

Terms of this equation are expanded based upon data for specific fishes. Computer simulations of the final model may be run to calculate growth, or consumption if the balance equation is rearranged. Many recent studies of fish popula-tions have used this basic modeling approach, successfully predicting growth or consumption (e.g., Kitchell et al. 1977; Kitchell and **Breck** 1980; Stewart et al. 1983; Rice and Cochran 1984; Stewart and Binkowski 1986).

Growth, the change in weight of predators between two

sampling times, must be known to estimate consumption of juvenile salmonids with a bioenergetics model.   Weight of individual, tagged predators could be recorded before and after the juvenile **salmonid** migration: however, tagging and recapturing adequate numbers of fish in a large system is difficult. Instead, the average weight change of aged cohorts between two sample times are typically used.   Estimating growth thus requires data on fish weight and age (from scales or other structures).

Consumption (C), the amount of food consumed by the fish, has the general form:

$$C = Cmax * P * F(T)$$

where:

Cmax = maximum specific consumption rate $(g \cdot g^{-1} \cdot d^{-1})$

P   = proportionality constant

T   = temperature (^{o}C)

F(T) = the temperature dependence function.

Cmax may be further defined as an allometric function of weight:

$$Cmax = a * W^{b}$$

where:

W   = fish weight (g)

a   = intercept of the allometric function for consumption, and,

b   = slope of the allometric function for consumption.

Several temperature dependence functions [F(T)] have been used in bioenergetic models (Hewett and Johnson 1987). An algorithm by Thornton and **Lessem** (1978) has been used for northern sguawfish (Vigg and Burley MS) and was used below. The Thornton and **Lessem** (1978) algorithm is essentially the product of two sigmoid curves, one fitting the increasing

portion of the temperature dependence curve (Ki) and one
fitting the decreasing portion of the curve (Kd):

$$F(T) = Ki * Kd .$$

The Thornton and **Lessem** model is best for cool- and cold-water
species (Hewett and Johnson 1987) and has been used for alewife
(<u>Alosa</u> <u>pseudoharenuus</u>), **coho** salmon (<u>Oncorhynchus kisutch</u>) and
chinook salmon (**O.** <u>tshawytscha</u>) (Stewart et al. 1981; Stewart
and Binkowski 1986). For more details on this function, see
Thornton and **Lessem** (1978) or Hewett and Johnson (1987:
Consumption Model 3).

Respiration (R), the amount of energy in weight equivalents
necessary to carry out standard and active metabolism, was
modeled as:

$$R = a * W^b * F(t) * ACT$$

where:
    W   = fish weight (g),
    a   = intercept of the allometric function for
respiration,
    b   = slope of the allometric function for respiration,
    F(T) = temperature dependence function, and,
    ACT = the increment for active metabolism.
    Activity (ACT) is modeled as a constant times the resting
metabolism: ACT is also called the **"Winberg** multiplier"
(Winberg 1956). Specific dynamic action (SDA), also required,
is calculated separately and added to respiration.
    The temperature dependence function for respiration of
Kitchell et al. (1977) was used in the northern sguawfish
bioenergetic model. This function (Respiration Model 2 of
Hewett and Johnson 1987) increases from 0 at low temperatures
to 1 at the optimum temperature (RTO) and back to 0 at the
maximum temperature (RTM).

Waste losses are egestion plus excretion. Egestion is fecal matter and excretion is nitrogenous waste products. The model also considers the caloric density of prey types and predator, weight loss during spawning, and water temperature · (see Hewett and Johnson 1987).

Methods

Growth - Since little is known about the seasonal growth pattern or the cold-water (<10°C, e.g.) physiology of northern sguawfish, all growth during a year was assumed to occur at temperatures above 10°C. The greater-than 10°C period at McNary Dam for 1983-86 was between April, 13 - November, 3, which was the period modeled. Carline (1987) also assumed growth only above 10°C when modeling largemouth bass.

Consumption - Vigg et al. (1988) and unpublished FWS analyses have noted increasing ration with increasing predator size for northern sguawfish in the BRZ of McNary Dam. Vigg and Burley (MS), however, did not find a significant effect of predator weight upon maximum consumption rate; most variation in their experiments was explained by temperature. We set the allometric consumption slope coefficient (CB) to 0 and the intercept (CA) to 0.4 (Table 3). CA was determined from Figure 4 of Vigg and Burley. Parameters of the temperature dependence function (Table 3) for consumption were fit by Vigg and Burley (MS) to laboratory feeding data with good success (R^2 = 0.97).

Respiration - No studies have been done on the metabolic requirements of northern sguawfish so data from related species (Sacramento sguawfish _Ptychocheilus arandis_; carp _Cyprinus carpio)_ were used where possible. Parameter values for ACT and SDA are "generic" values used for a variety of predators in previous studies (Hewett and Johnson 1987). Table 4 lists parameters used in initial model exercises.

Waste Losses - Egestion was modeled as a constant proportion of consumption (Kitchell et al. 1977) while

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Table 3. Consumption parameters used in bioenergetic modeling of northern sguawfish. Parameter names are the same as those used by Hewett and Johnson (1987).

Parameter	Value	Description	Source
CA	0.4	Intercept for max. cons.	Based on Vigg & Burley (MS)
CB	0.0	Coefficient for max. cons.	Based on Vigg & Burley (MS)
CQ	0	Temp. when dep. equals K1	Vigg & Burley (MS)
CTO	21.5	Temperature for optimum cons.	Vigg & Burley (MS)
CTM	21.5	Temp. for opt. consumption	Vigg & Burley (MS)
CTL	27	Upper temp.	Vigg & Burley (MS)
CK1	0.001	Temp. depend. lower	Vigg & Burley (MS)
CK4	0.01	Temp. depend. upper	Vigg & Burley (MS)

Table 4. Respiration parameters used in bioenergetic modeling of northern sguawfish. Parameter names are the same as those used by Hewett and Johnson (1987).

Parameter	Value	Description	Source
RA	0.0108	Intercept for respiration	Hewett & Johnson (1987)
RB	-0.20	Coefficient for respiration	Basu (1959)
RQ	2.44	Q_{10} at 10-25 deg	Calculated from Cech et al.(1990)
RTO	27	Temperature for optimum resp.	Black (1953)
RTM	29	Max. temperature when resp.=0	Black (1953)
ACT	1.0	Activity	Hewett & Johnson (1987)
SDA (S)	0.172	Specific Dynamic Action	Hewett & Johnson (1987)

excretion was considered a constant proportion of consumption minus egestion; egested calories cannot be excreted. Previous studies (Hewett and Johnson 1987; **Bartell** et al. 1986, e.g.) indicate that proportional descriptions of waste are probably · adequate for modeling growth or consumption. The egestion parameter (FA) used was 0.104 (largemouth bass: Hewett and Johnson 1987; Rice et al. **1983),** while **the excretion** parameter (UA) was 0.068 (largemouth bass: Hewett and Johnson 1987).

Northern **Squawfish** Diet - Four diet categories (salmonids, non-salmonids, invertebrates, and miscellaneous) were considered in the model. For all years (1983-86) and months (April-August) combined, salmonids were 66.7% of the diet, **non-salmonid** fish were **14.2%,** and invertebrates, mostly crayfish, were 16.3% (Poe et al. 1988). A monthly summary of diet categories and caloric densities is provided in Table 5. Diet composition varied by time of year and by predator size (Poe et al. 1988; FWS unpublished data).

An age-at-length key for northern squawfish in John Day Reservoir (Vigg et al. 1988) was used to assign ages to unaged, but measured, fish for diet analyses. Weight (g) was estimated from length (mm), when required, based upon a relationship computed from 5,460 northern squawfish collected in John Day Reservoir and in John Day Dam tailrace:

$$\text{Weight} = 10^{-5.116} * \text{Length}^{3.085} \qquad R^2 = 0.98 .$$

Caloric Density - Caloric density of spring chinook smolts was estimated at selected locations during their outmigration and found to be similar between Priest Rapids Dam and Jones Beach (Rondorf et al. 1985). An energy density of 1,030 calories/g wet weight (Rondorf et al. 1985) was used for juvenile salmonids throughout the simulation period. Energy density of non-salmonid fishes was set to 1,000 **cal/g** (Hewett and Johnson 1987). Invertebrates in the diet were primarily amphipods (<u>Coronhium</u>) and crayfish (Poe et al. 1988). Amphipods have an approximate energy density of 934 **cal/g** and decapods 1,077 **cal/g** (Cummins and Wuycheck 1971; Stewart et al.

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Table 5.   Proportions of major diet categories in northern
sguawfish guts collected from John Day Reservoir and **tailrace**
during 1983-1986.   The **"Other"** category was plants, detritus
and unidentifiable material.

Diet Category	**Apr**	**May**	Jun	Jul	**Aug**
Salmonids	0.676	0.726	0.461	0.810	0.438
Non-salmonids	0.194	0.121	0.166	0.072	0.233
Invertebrates	0.101	0.129	0.322	0.106	0.291
Other	0.026	0.022	0.050	0.010	0.036
N	566	1072	1192	875	1077

1983) ; the invertebrate food category was assigned an energy
density of 1,006 **cal/g.**   The **"Other"** diet category was assumed
to be largely indigestible material **(chitin,** scales, insects,
plant material, etc.) and was given an arbitrary energy density
of 500 **cal/g.**

Northern sguawfish caloric density is not known and was set
to 1,000 **cal/g** (Hewett and Johnson 1987).   Seasonal changes in
caloric density of the predator can be modeled, but lack of
data prevented such detailed efforts in the present model.

Spawning Losses - Weight loss due to spawning can be
accounted for in the northern sguawfish bioenergetic model.
Jeppson and Platts (1959) estimated fecundity and gonad weight
in gravid northern sguawfish females in Idaho and found that
"In larger female sguawfish, eggs may total 100,000 or more,
averaging **[12.5%]** of the body weight".   They observed spawning
during a one month period in late spring or early summer.   In
John Day Reservoir, spawning occurred in June through early
July, while the gonadosomatic index peaked at about 7% for
females and 3% for males (Vigg and Prendergast, unpublished
MS) .   Female northern sguawfish in the reservoir lost about 6%

of their body weight between June 9, 1982 and mid-July, 1982.
Spawning weight loss in the model was set to 6% of total body
weight and occurred on June 15th. All cohorts modeled were
assumed to be mature adults.

Temperature - Average monthly temperature was calculated
from Army Corps of Engineers data collected at McNary Dam (ACOE
1983-1986).

Sensitivity Analysis - To guide further model development,
sensitivity of model output to individual bioenergetic
parameters was examined. Simulations were for a single cohort
of 8-year old northern sguawfish; 8-year old fish were chosen
since they weighed about 626-779 g (Vigg et al. 1988), which
included the mean weight of all fish captured in John Day
Reservoir (772 g; Vigg et al. 1988). Sensitivity was explored
by individually varying parameters ±10% and comparing
accumulated smolt consumption (g) with a standard simulation.
Temperature parameters were varied by ±1°C. Parameter values
in the standard simulation were described above and are listed
in Tables 4-6.

Parameter sensitivity was calculated by the method of
Kitchell et al. (1977); this method has also been used in other
bioenergetic studies (Bartell et al. 1986; Adams and DeAngelis
1987). Sensitivity values were normalized to the standard
simulation by:

$$S(P) = (p * \Delta x) / (x * \Delta p)$$

where S(p) = sensitivity for parameter p,
       p ≈ standard parameter value,
  delta p ≈ input deviation of parameter p,
       x ≈ standard value of accumulated consumption, and,
  delta x ≈ deviation of accumulated consumption due to
            delta p.
A sensitivity of 1.0 means that a parameter change of 10%
produces a 10% change in the output variable. Efforts to

improve the bioenergetics model would be focused on parameters
with high sensitivities, where small errors could cause the
largest change in model output.

Sample Size Requirements - Approximate sample sizes were
calculated to answer the question: "How many fish within an age
group are required to detect weight changes during spring or
summer sampling periods?". Three potential sampling intervals,
from May to July, July to September, and May to September, were
examined (Table 6). Predicted weights from the simulations on
three dates (May 15, July 15 and September 15) were used to
calculate sample sizes. Standard deviations of predicted
weights, which were necessary for sample size calculations,
were estimated using aged northern sguawfish (N=266) collected
in John Day Reservoir during 1985 (ODFW, data provided by BPA).
The mean coefficient of variation for age-specific weights
during 1985 (26.7%) was used to compute standard deviations of
weights on sample dates. Weights were assumed to be normally
distributed about the mean.

Results

Seasonal Growth - For the period modeled (April 13-
November 3), individual predators first showed a gradual weight
loss followed by a rapid increase in weight during July, August
and September (Figure 4). Spawning in June produced a small
weight loss, which was rapidly recovered (Figure 4). This
pattern of weight change was probably driven largely by water
temperature in the river. Average temperature at McNary Dam
during 1983-86 increased from about $9^{o}C$ in April to over $15^{o}C$
in June; July through September temperatures were over $19^{o}C$
(data from ACOE).

Smolt consumption increased rapidly in the spring to a
maximum during July (Figure 4), when 5-6 g of juvenile
salmonids were consumed in a day by an 8-year-old northern
sguawfish. The spring outmigration of smolts was not obvious

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Table 6. Number of aged northern sguawfish necessary to distinguish seasonal weight changes during three periods. Type I error was set to **.05,** Type II error was **.10,** and a one-tailed test was specified.

Age	Sample Period					
	May - July		July - September		**May** - September	
	Sample Size	Percent Weight Change	Sample Size	Percent Weight Change	Sample Size	Percent Weight Change
4	84	8.6	7	30.4	4	41.6
5	89	8.2	8	28.7	4	39.2
6	166	6.1	13	22.3	7	30.0
7	249	5.1	17	19.3	10	25.2
8	274	4.7	18	18.6	11	24.2
9	325	4.3	20	17.5	12	22.6

in the specific consumption curve (Figure **4),** possibly because metabolic needs were lower when water was cool.

Ration Comparisons - To make some comparisons of predicted and observed consumption rates, the bioenergetics model was run using data specific to John Day Reservoir during 1983-86. Total ration and **salmonid** ration for 8-year-old northern sguawfish predicted by the model were compared with ration estimates made in the Boat Restricted Zone and the pool of John Day Reservoir by Vigg et al. (1988). Vigg et al. (1988) sampled over 4,700 northern sguawfish and estimated consumption by a modification of the Swenson and Smith (1973) technique.

Total ration predictions by the bioenergetic model were fairly close to estimates for the John Day pool, except during May (Figure 5). In May, total ration in the pool (18 $mg \cdot g^{-1} \cdot d^{-1}$) was over twice that predicted by the bioenergetics model (7 $mg \cdot g^{-1} \cdot d^{-1}$). During other months, there was less than a 4 $mg \cdot g^{-1} \cdot d^{-1}$ difference between the model and field data. The
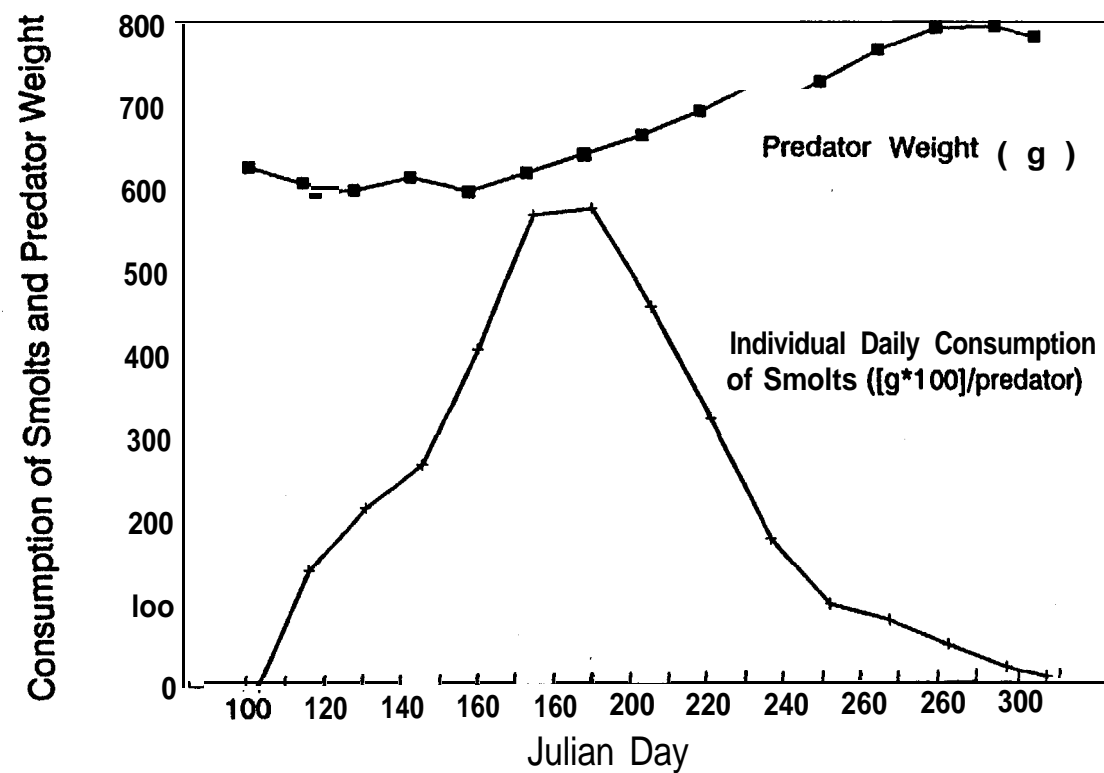
Figure 4. Northern squawfish weight and daily consumption of smolts predicted by the bioenergetics model. Simulation was for an 8-year-old predator and results were plotted for each 15 days between April 13 and November 3 (the greater-than 10°C period).

Figure 5. Comparison of rations predicted by the bioenergetics model with data collected in John Day Reservoir during 1983-86. Model predictions were for an 8-year-old fish sampled on the 15th day of the month. Total ration and salmonid ration were taken from Vigg et al. (1988: Figs. 2 and 3). The reservoir was divided into Boat Restricted Zone (BRZ) and Pool.

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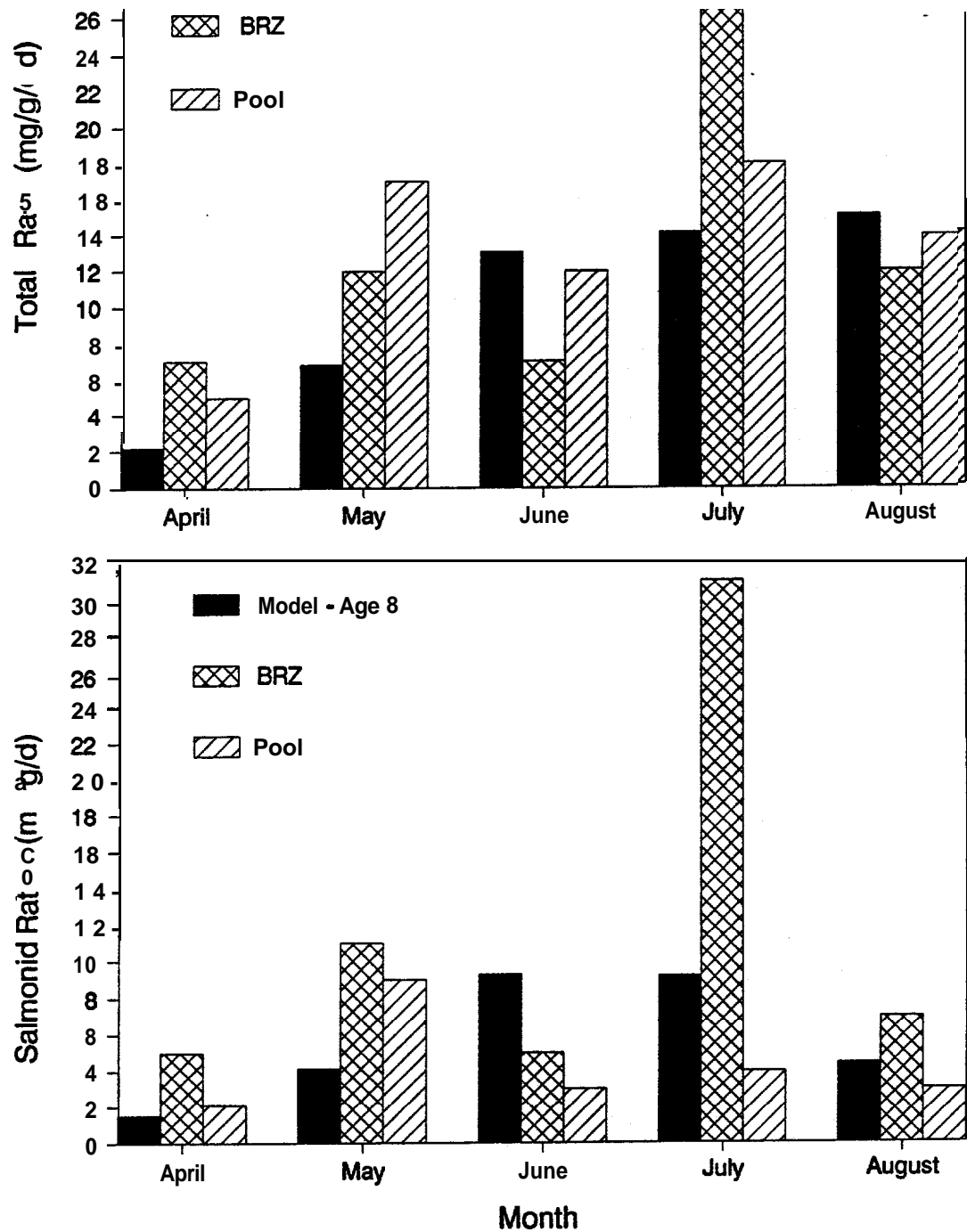model was less effective at predicting ration within the BRZ, especially in July when consumption was very high in the Boat Restricted Zone. **Salmonid** ration predictions and observations were similar to those for total ration, although the June prediction was also higher than observed consumption in both the pool and BRZ (Figure 5).

Sensitivity Analysis - Consumption of juvenile salmonids in the model was most sensitive to respiration parameters (Figure **6).** Deviations of several respiration parameters produced relatively large changes in smolt consumption, while variation in maximum consumption, excretion, and egestion parameters produced relatively small changes in the output. Accumulated **salmonid** consumption was most sensitive to the maximum temperature at which respiration was zero (RTM), where a $-1^{o}C$ change caused consumption to change **by** about 25% (Figure 6). Consumption was moderately sensitive to the activity parameter (ACT) and to the caloric density of northern sguawfish.

Ageing - Some ageing of northern sguawfish in the Columbia River has been done by (Beamesderfer et al. 1987); no ageing was done during the current project. Beamesderfer et al. (1987) found northern sguawfish as old as 17 years by counting scale **annuli.** During 1983-86, median age, after adjusting for gear vulnerability, ranged between 4 and 9 years old (Beamesderfer et al. 1987). Reader agreement between separate age determinations was variable but declined with increasing age. Experienced readers had over 50% agreement on age determinations when fish were 9 years old or less.

For bioenergetics modeling, northern sguawfish would be categorized into six age groups: 4 years or less, 5, 6, 7, 8, and greater than 8 years. Four-year-old fish are just large enough to consume outmigrating juvenile salmonids (Poe et al. 1988; Vigg et al. 1988). Fish older than 8 years were relatively hard to age by counting scale **annuli** (Beamesderfer et al. 1987); also, consumption rate differences between older fish are probably small, compared to younger, faster-growing
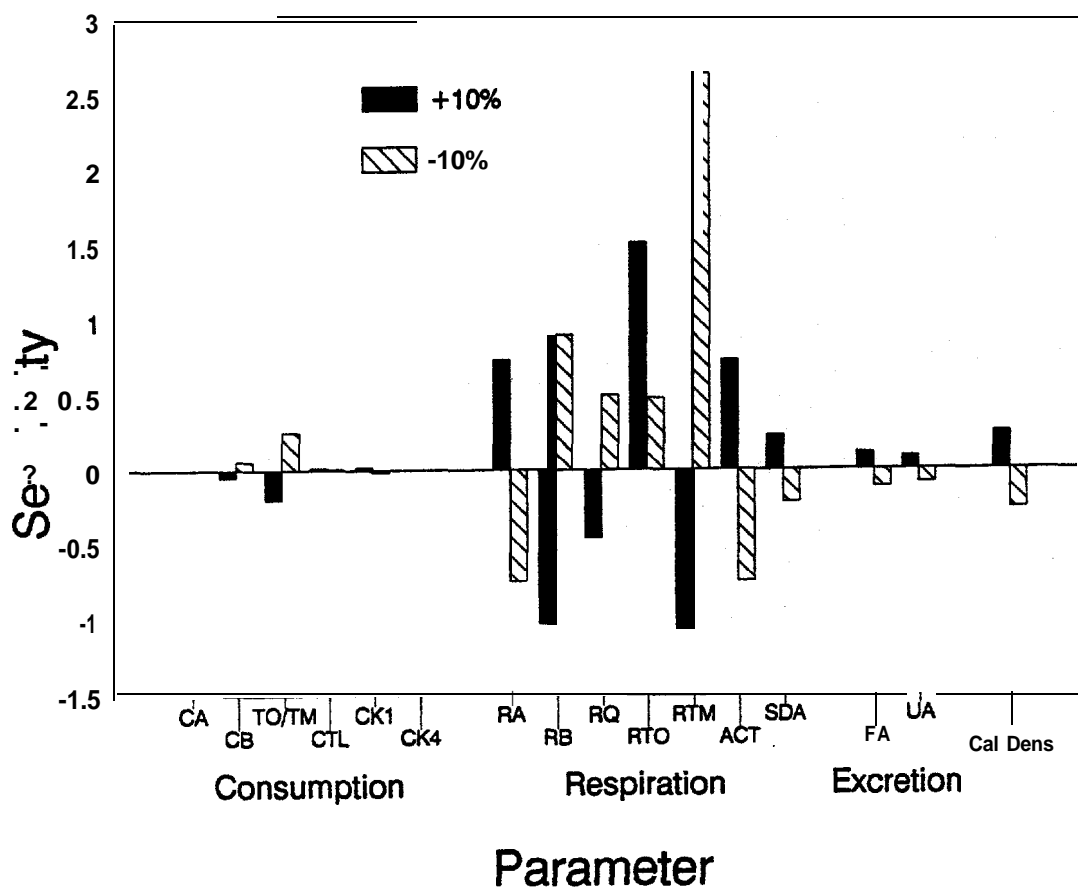
Figure 6. Sensitivity of the northern squawfish bioenergetic model to
±10% deviation in input parameters. Accumulated smolt consumption
between April and October was the tested output variable. Temperature
parameters were varied ±1°C, rather than 10%. Parameter names,
descriptions and standard values are described in the text. "Cal
dens" refers to predator caloric density.

individuals.   Grouping age 8 and older fish would also reduce
the amount of effort required to age very old fish.   Otoliths
and other bony structures will be examined for possible use in
ageing work and to verify scale-ageing methodology.

Sample Size Requirements - Minimum sample size varied
depending upon the growth interval examined (Table 6).   The
proportional growth of individuals between May and July was
relatively low (see Figure 4, e.g.), being about 4-9% depending
upon fish age: the sample sizes required to detect this
difference were large (Table 6).   Between July and September,
the percent weight change was much higher (17-30%; Table 6),
and fewer individuals would be needed to detect this change,
compared to the May-July period.   Simulated growth from May to
September was greatest and less than 20 fish per age class
would be required to detect seasonal growth changes from May to
September (Table 6).   Older age groups required larger samples
since the proportional weight change declined with increasing
age.

Discussion

Ration comparisons of model predictions and field data were
meant as a rough guide to potential model performance.   A more
complete analysis would include all age classes and the
proportions of the population within each age class.   The above
comparisons do, however, suggest that bioenergetic modeling has
good potential for estimating consumption, especially within
the pool of a reservoir.   The slightly poorer performance of
the model for predicting salmonid rations suggests that diet
proportions and caloric densities of prey types and predator
should be re-examined.

Consumption estimation using bioenergetic models has been
shown in several studies to be sensitive to respiration
parameters, and relatively insensitive to maximum consumption
parameters (Kitchell, 1977; Stewart et al. 1983; Cui and

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Wootton, 1989). **Bartell** et al. (1986) concluded that a model
of alewife consumption was most sensitive to the temperature
dependence of respiration and consumption, requiring accurate
data on the thermal history of the fish. Results of our   -
sensitivity analysis, and the shortage of species-specific
metabolic data (Table **5),** suggest that respiration experiments
could improve the bioenergetics model.

Although sample size estimates were approximate, requiring
assumptions about seasonal growth patterns and variance about
the mean weights, some conclusions could be drawn. The
bioenergetics approach would probably not allow separation of
consumption into early and late-season components because of
sampling considerations. Estimates of consumption for the
early smolt outmigration period (April-June) would not be
feasible due to slow predator growth and the large sample size
needed to detect growth. Bioenergetic-based consumption
estimates should be only for spring-fall or summer-fall periods
when the growth increment is relatively large and detectable
with about 20 fish per age group.

SECTION II.   PREDATOR-MOLT DYNAMICS

Three aspects of predator-smolt dynamics were included as
tasks in the 1989-90 study plan. Additional data were needed ·
on the functional relationship between predators and prey to
accurately model and understand the interaction and the
influence of physical parameters.

The Columbia River Ecosystem Model (CREM) was developed for
John Day Reservoir to explore predation and evaluate predator
control efforts. CREM was based primarily upon the functional
response of predators to varying prey density. Further data
were needed to refine the functional response relationship and
to test assumptions of the model. Other modeling approaches
were also being considered by researchers in the region and
discussion was necessary to resolve problems and plan effective
programs. The three parts of this Section address some of
these problems.

Maximum Consumption Experiments

Experiments to measure the maximum consumption rate of
northern sguawfish within the laboratory were completed and a
manuscript (Vigg and Burley MS) has been submitted for
publication.   See Appendix A.

Predator-Prey Modeling Workshop

A workshop was held in May, 1989 to discuss modeling
approaches and problems related to predator-prey dynamics in
the Columbia River. The workshop was coordinated by a steering
committee that included Jim Petersen (committee chairman) and
Tom Poe of the FWS. Results of the workshop have been
published as a separate Bonneville Power Administration report
(Fickeisen et al., 1990).

Introduction

The functional relationship between prey density and predator consumption rate is an important prerequisite to understanding and modeling predator-prey dynamics. Earlier work on juvenile **salmonid** predation within John Day Reservoir (Poe and Rieman, 1988) provided data on.the functional response of predator consumption rates to prey density (Vigg 1988). In general, consumption rates increased in a nonlinear manner as smolt density increased, reaching an asymptotic rate of about **five** smolts per predator per day when smolt density was very high. The transition and asymptote of the functional response were, however, defined by relatively few data points (Vigg 1988; his Figure 4, e.g.).

Since the functional response of predator consumption rate is central to current predation models and interpretations (Beamesderfer et al. 1988: Poe et al. 1988; Vigg 1988; Fickeisen et al. **1990),** definition of the shape and asymptote of this function are crucial. Therefore, we initiated a limited effort to collect data on northern sguawfish consumption that would supplement existing data and further define the functional response curve. This section reports our efforts to refine the functional response curve.

Methods

Northern sguawfish were sampled within the **McNary** Dam boat restricted zone on nine days during July, 1988 (Table 7). Predators were collected through the diurnal period by electroshocking at stations near the navigation lock guidewall, the outlet of the smolt bypass, the spill gates and on the Oregon shoreline. Field methods, laboratory methods, and data analyses were described in earlier predator-prey studies (Poe

et al. 1988; Vigg et al. 1988).

Calculations of consumption by northern squawfish were
based upon the method of Swenson and Smith (1973) as modified
by Vigg et al. (1988). Calculation of smolt density for the ·
McNary BRZ used Migrational Index (MI) data from McNary Dam
(Fish Passage Center, **1988),** daily flow at McNary Dam (Koski et
al. 1989) and formulae in Vigg (1988). Variability in daily
consumption was estimated by the bootstrap resampling technique
(Efron 1982; Boisclair and Leggett 1988). Briefly, data sets
of daily predator records were resampled by computer to
generate new record combinations for consumption calculation.
Each resample contained the same number of predator records as
the original sample (Efron 1982). The original data were
resampled 500 times to produce a frequency distribution of
consumption rates for a given day.

Results

During nine days of sampling, 607 northern **squawfish were**
captured (Table 7). Catch per effort during night (1900-0700
hours) was about 23 predators/hour, compared to 14
predators/hour during the day (0700-1900 hours). Water
temperature at McNary Dam increased less than 1°C during the
11-day sampling period (Table 7).

Smolt passage at McNary Dam during the summer of '1988 had
several peaks, with the largest occurring in late June (Figure
7). Although our sampling missed the highest passage, fish
collected between July 18-20 coincided with a fairly high
period of smolt passage (Table 7; Figure 7). Collections made
from July 14-16 occurred during a time of intermediate,
declining passage and sampling from July 22-24 was during a
period of relatively low passage.

Ration and **salmonid** consumption rate were estimated for
each collection day (Table 8); number of fish used in
consumption analyses was less than the total catch because of

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Table 7. Summary of northern squawfish catch, water temperature and passage index at McNary Dam for sampling dates in July, 1988. Temperature data are from Army Corp of Engineers and juvenile **salmonid** passage data are from the Fish Passage Center.

Date	Total Catch of Northern Squawfish	River Temgerature (C)	Juvenile **Salmonid** Passage Index at McNary Dam
7/14/88	104	19.4	164,460
7/15/88	57	19.4	93,160
7/16/88	26	18.9	52,300
7/18/88	78	18.9	163,634
7/19/88	114	18.9	256,900
7/20/88	40	20.0	170,599
7/22/88	58	20.0	29,585
7/23/88	105	20.0	26,133
7/24/88	25	20.0	23,467

size requirements (only predators $\geq$ 250 mm were included) and exclusion of torn or damaged guts. Analyses for daily sample size requirements (see Section I of this report, Direct Consumption Indexing) suggested that 15-30 northern squawfish per day was adequate to describe consumption variation. The minimum number of northern squawfish in a daily sample during July, 1988 was 20, with most sample days having over 40 predators (Table 8).

Salmonids constituted from 73% to 99% (mean 91%) of the northern squawfish diet during the nine sample days in July 1988. During the period of highest consumption (July **18-20)**, the predator's diet was almost completely salmonids (96-99%). Vigg (1988) also observed a high proportion of smolts in the diet of northern squawfish when density of juvenile salmonids was high.

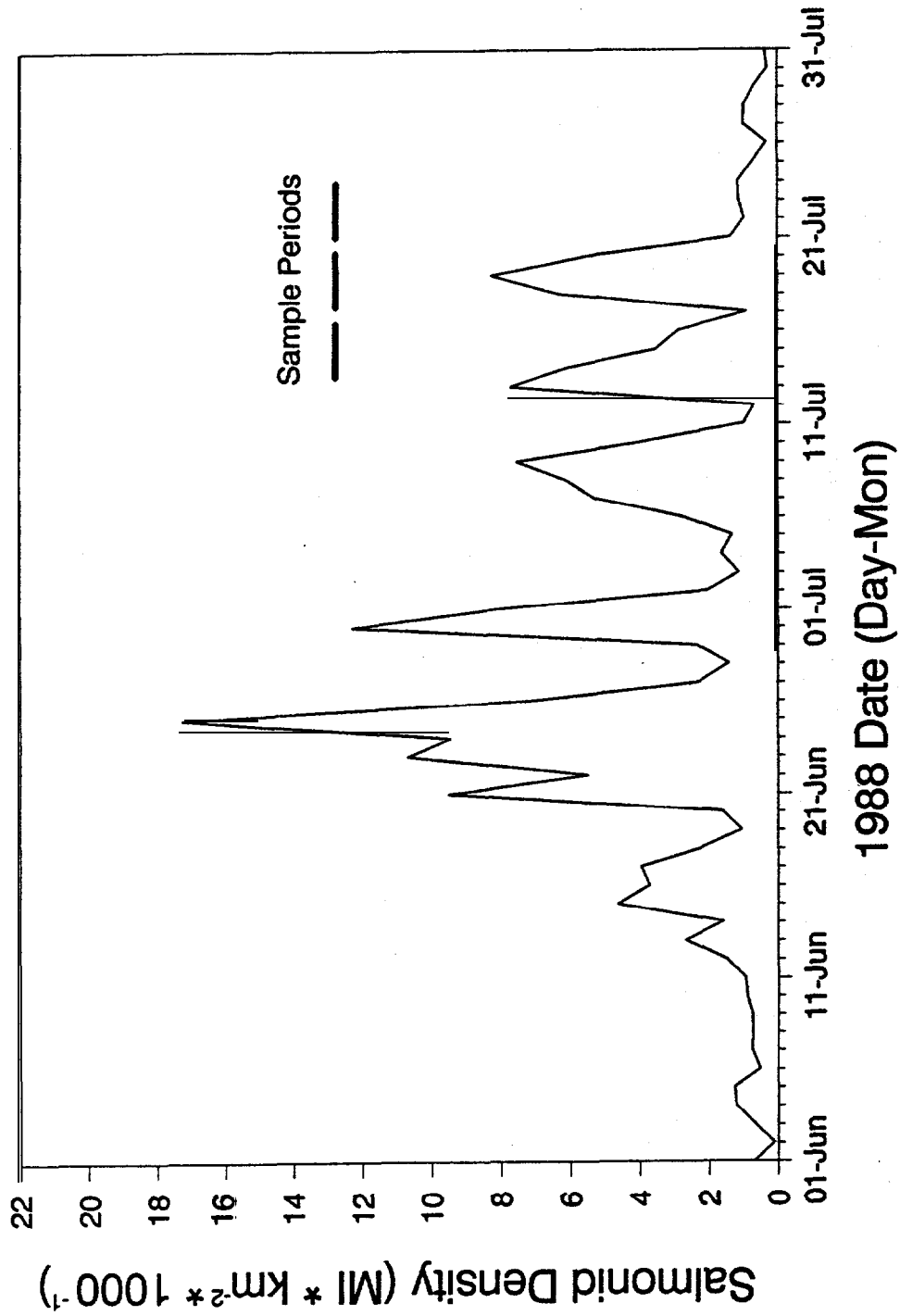Total daily ration (Table 8) for northern squawfish varied

Figure 7. Smolt density in the McNary BRZ during June and July, 1988. The three 3-day sampling periods are also shown.

Table 8. Total daily ration, **salmonid** ration and **salmonid** consumption
rate for northern sguawfish in the **McNary** Dam **tailrace** during July,
1988. Bootstrap analyses were done on each sample date to estimate
standard deviations, which are shown in parentheses.

Date	# of Predators	Total Ration $(mg \cdot g^{-1} \cdot d^{-1})$	**Salmonid** Ration $(mg \cdot g^{-1} \cdot d^{-1})$	**Salmonid** Rate (smolts' predator-" d")
7/14/88	94	19.4 (3.7)	18.5 (3.8)	1.27 (0.28)
7/15/88	50	30.3 (8.3)	28.4 (8.0)	1.84 (0.58)
7/16/88	21	12.0 (6.2)	8.8 (5.6)	0.40 (0.27)
7/18/88	53	74.6 (12.9)	73.9 (12.9)	4.39 (0.90)
7/19/88	98	78.8 (7.3)	75.9 (7.7)	4.20 (0.59)
7/20/88	47	42.7 (6.1)	42.3 (5.9)	2.24 (0.41)
7/22/88	52	12.9 (4.5)	11.3 (4.3)	0.55 (0.21)
7/23/88	95	13.4 (2.8)	10.4 (2.7)	0.42 (0.10)
7/24/88	20	15.5 (4.5)	14.9 (4.9)	0.69 (0.21)

Table 9. Functional response parameters for data **(n=32)** from late
June through August of 1983-86 and July, 1988. Parameters were fit by
nonlinear, least-squares regression.

Equation: Consumption = Cmax **/ [1** + {a * exp(b ***** Smolt Density)}]

Parameter	Estimate	Standard Error
Cmax	3.915	0.664
a		
b	10.951 -0.618	4.828 0.194

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from 12 mg prey per g predator (July 16) to over 78 mg prey per g predator (July 19). Daily variation in **salmonid** ration and number of salmonids consumed per day was closely correlated with total daily ration (Table 8). Variability of the bootstrap distributions was also similar for the three estimated rates (Table 8); coefficient of variation of the mean was less than **40%,** except for July 16 when the coefficient of variation was as high as 67% . Bootstrap distributions of total ration, **salmonid** ration and **salmonid** consumption rate were tested for normality by chi-square tests. About half (12 of 27) of the tested distributions were significantly different from a normal distribution, being skewed toward low rations or rates.

A functional response curve was fit to consumption rates estimated during July, 1988 and late June-August, 1983-86. All sample dates later than June 20 with 15 or more predators ($\geq$ 250mm) were selected from the 1983-86 database. Most dates were in July or August, but four days in late June **(23-26)** of 1986 were also included. A total of 32 daily consumption estimates were analyzed. Data were fit to an exponential sigmoid function of the form:

Consumption = Cmax **/[1 + {a** * exp(b * **Smolt** Density))] **(1)** .

Equation parameters are given in Table 9 and data are plotted in Figure 8. Analysis of variance for the regression was highly significant **(F=41.6;** df **3,29;** P < **.001)** and about 66% of the variation was explained.

Discussion

The maximum rations and rates observed on July 18-19 were comparable to maximums estimated in predator-prey studies for 1983-1988 (Vigg et al. 1988; Vigg 1988). During the earlier studies, maximum **salmonid** consumption rate was about 5 smolts ·
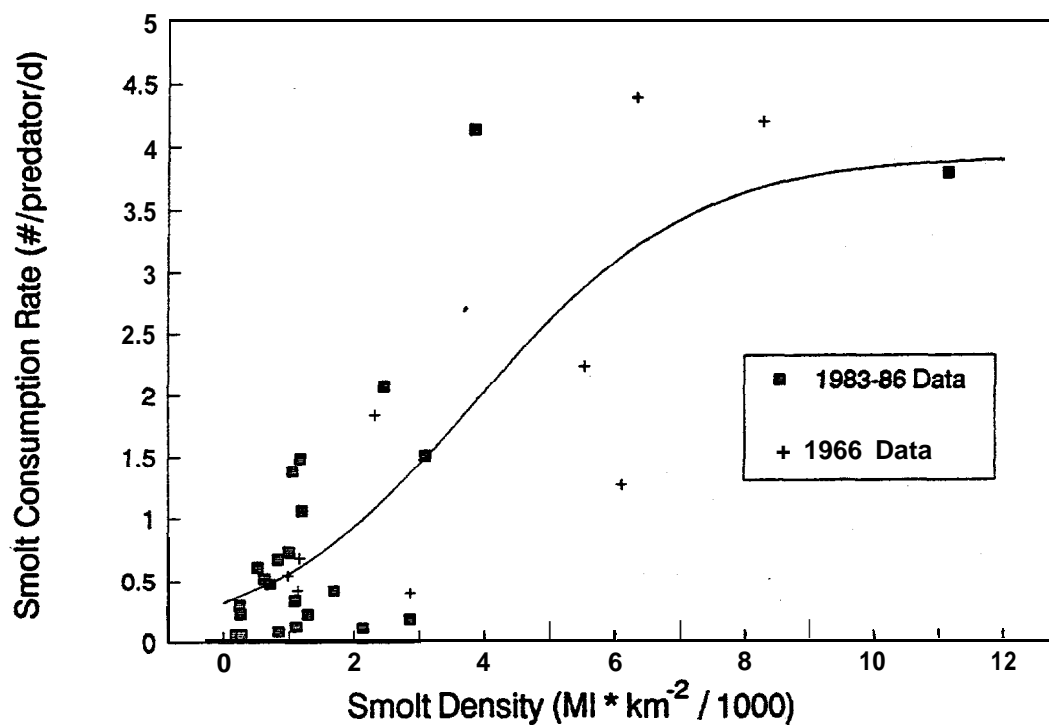
Figure 8.   Smolt consumption rate by northern squawfish as a function
of smolt density in the **McNary BRZ.** Data are from late June through
August of 1983-86 and July 1988.   The functional response curve was
fitted to the data using an exponential sigmoid equation (see text
and Table 9).

northern **squawfish**$^{-1}$. **d**$^{-1}$ and maximum **salmonid** ration was
roughly 65 mg **salmonid** · g northern **squawfish**$^{-1}$· **d**$^{-1}$ (Vigg 1988,
his Figure 4). During 1988, maximum consumption rate was 4.4
smolts . northern **squawfish**$^{-1}$ · **d**$^{-1}$ and maximum **salmonid** ration ·
was 76 mg **salmonid** . g northern squawfish" · **d**$^{-1}$ (Table 8). The
lower consumption rate but higher ration in 1988, compared to
Vigg's (1988) results, suggest that the juvenile salmonids
during 1988 were slightly larger than those consumed during
1983-86.

Consumption data from 1988 refined the shape and asymptote
of the functional response curve, particularly at intermediate
and high juvenile **salmonid** densities (Figure 8). At low
salmonid densities, the 1988 results were similar to earlier
data. Between smolt densities of 3000-6000 **MI/km**^{2}**,** consumption
estimates were fairly scattered, as might be expected since
consumption changes rapidly within this range. Four estimates
of consumption, over a broad range of prey densities, were near
4 smolts · northern squawfish-' · **d**$^{-1}$**,** apparently representing
maximum daily consumption for **"average"** predators. Addition of
July, 1988 data for this analysis **provides** **two** new values to
define the asymptote of consumption and, also, a couple of
values in the mid-density range. Future analyses of functional
response relationships of northern squawfish should also
benefit from the July, 1988 data set.

SECTION III.   SELECTIVE PREDATION

The U.S. Fish and Wildlife Service (FWS) and the Oregon
Department of Fish and Wildlife (ODFW) recently completed a six
year study to determine the significance of predation on
juvenile salmonids in John Day Reservoir. Study results
indicated that predation may account for the majority of
previously unexplained smolt mortality and that northern
squawfish was the dominant predator (Poe and Reiman 1988).
Northern squawfish consumption rates on juvenile salmon were
significantly greater and their abundance was from 12 to 18
times higher in the boat restricted zone (BRZ) below McNary Dam
than in other areas of the reservoir (Beamesderfer and Rieman
1988: Vigg et al. 1988). These results suggest that northern
squawfish may be selecting smolts that are killed, injured,
stressed, or disoriented as a consequence of dam passage. If
northern squawfish are selective for certain types of prey or
substandard (sensu Temple 1987) prey are more vulnerable to
predation, the overall significance of predation as a mortality
factor must be reassessed.

Studies of feeding preferences are fundamental to
understanding basic trophic relationships and can help define
the functional role of predaceous fishes. Selective predation
occurs when the relative frequencies of prey types in the
predator's diet differ from the relative frequencies in the
environment (Chesson 1978). Prey vulnerability, as an adjunct
to selective predation, may be the primary determinant of what
actually is eaten (Allen et al. 1987).

There is substantial literature on selective predation by
fish, with the emphasis on prey size (Wright 1970; Werner and
Hall 1974; Post and Evans 1989) or species selection (Espinosa
and Deacon 1973; Hargreaves and Le Brassuer 1985; Wahl and
Stein 1988). Several investigators have found that various
stressors, including exposure to temperature shock or
contaminants (Hatfield and Anderson 1972; Coutant 1973; Coutant

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et al. **1974),** handling (Olla and Davis **1989),** and crowding (Congleton et al. 1985) increased the vulnerability of prey to predators. Out-migrating juvenile salmonids exhibit a variety of physiological and morphological conditions due to disease, · stress, and physical injury (Maule et al. 1988; Koski et al. 1989; Rondorf et al. 1989). Dam passage related and multiple cumulative stresses have been shown to maximally stress salmonids (Barton et al. 1986; Maule et al. **1988),** perhaps rendering them unable to cope with subsequent stresses such as predation. Although the theory of selection upon substandard individuals is widely accepted, evidence supporting such a theory is scarce (Temple 1987).

The objectives of this work were to develop the laboratory and field protocols necessary to evaluate predator selection and prey vulnerability. To address these objectives, we designed and constructed laboratory systems and conducted preliminary experiments on selective predation by northern squawfish on three categories of substandard vs. standard juvenile salmonids: dead vs. live: injured vs. non-injured; and stressed vs. unstressed. To conduct selective predation experiments in a more realistic environment, we planned some experiments using net pens anchored in backwaters of the Columbia River. Although we obtained net pens and located potential test sites, subsequent agency review precluded us from conducting any field experiments.

Methods

Test fish.-Northern sguawfish **(>275** mm FL), collected from the Columbia River by electroshocking, were used as predators for all experiments. Fish were acclimated in the wet laboratory (described below) for 3 weeks prior to experiments. During the acclimation period and between experiments, northern sguawfish were fed a maintenance diet of live juvenile **coho** salmon Oncorhvnchus kisutch from the Willard National Fish

Hatchery.

Subyearling spring chinook salmon $\underline{O}$. tshawytscha (average weight 10.8 g ± 0.2 g SE; average length 96.0 mm ± 0.6 mm SE) from the Little White Salmon National Fish Hatchery were used - as prey in all experiments and as test fish in stress evaluations (see below). Fish were maintained in either the wet laboratory or in outside circular tanks receiving well or river water. Both chinook and **coho** salmon were fed a maintenance diet (0.7% body weight/day) of **BioMoist** feed.

W-Several variables are important to selective predation experiments, including water temperature, photoperiod, numbers of predators and prey, experiment duration, and predator starvation period. This section briefly describes the derivation of variables for our selective predation experiments: unless noted, the values stated below were used in all experiments.

We used water temperatures of **15-17°C** for all experiments. Beyer et al. (1988) reported that northern sguawfish feed well at these temperatures and the range approximates Columbia River water temperatures during early to mid-summer periods. Photoperiod for all experiments was set at 15-h-daylight and **9-**h-darkness. We used relatively low light levels (3.2 lux) during daylight periods because preliminary experiments revealed northern sguawfish did not feed well in bright light. Either two or three predators were used in experiments conducted in circular tanks (see below); we noted in earlier trials that northern sguawfish appear to be rather social and do not feed well in isolation. The number of prey offered to predators was set at 10 of each treatment group per predator. This number is twice the maximum consumption rate reported for northern sguawfish (Appendix A) and would prevent any problems with prey depletion or total prey consumption. We typically allowed predation to proceed for 24 h, a time frame covering the **diel** cycle and often used in other studies (Congleton et al. 1985; Wahl and Stein 1988). We chose 48 h for our predator

starvation period to ensure high feeding motivation.   This
period was based upon maximum prey intercapture times of
northern sguawfish calculated from field data (USFWS,
unpublished data).

Live vs. Dead Selection Experiments

     Experimental apparatus.-All experiments were carried out
in 1.5 m diameter flow-through circular tanks receiving an
input flow of 19 L/min. Water was recirculated by two
centrifugal pumps, heated by an electric heater, and sterilized
by ultraviolet light. Water was also passed through a bio-
filter to remove ammonia and other particulate waste. Lighting
was provided by six 50-W incandescent lights set on timers to
control photoperiod. Lights were aimed toward the ceiling to
provide indirect light intensities of 3.2 lux at mid-water
level. A complete description of this laboratory is given by
Lucchetti and Gray (1988).

     Experimental design.-To begin an experimental trial, three
northern sguawfish were stocked in each of six circular tanks
and allowed one week to acclimate. On the morning following
predator starvation, 180 chinook salmon were killed by a blow
to the head and given an adipose fin clip to distinguish them
from live prey should any live prey die during the experiment.
Live and dead prey (30 of each) were then introduced
simultaneously into each tank and predation allowed to proceed
for 24 h. All remaining prey were identified and enumerated at
the end of each trial. Each tank was considered a replicate:
we conducted 3 trials of this experiment, each with 6 tanks,
for a total of 18 replicates. For each trial, either new
predators were used, or fish were moved among tanks to minimize
habituation or learning. Experiments were conducted from July
to September, 1989.

     A one-way analysis of variance failed to reveal any time
or tank effects during the experiments, therefore all data were

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combined for analysis. A 2 x 2 contingency test of proportions (z) using arc sine transformed data (Snedecor and Cochran 1980) was used to test the hypothesis that the proportions of dead and live prey consumed were equal.

Injured vs. Non-injured Selection Experiments

The same laboratory as described above was used to conduct these experiments. We used descaling to injure prey because descaling is widespread in out-migrating juvenile salmon and its effects on their vulnerability to predation are unknown. Because of the amount of time required to manually descale fish, we reduced the number of predators to two per tank and therefore used fewer **prey** fish.

We conducted three different trials of this experiment: 50% descaling with a 1 h recovery; 50% descaling with a 24 h recovery; and 20% descaling with a 1 h recovery. We replicated the 50% descaling trials three times and the 20% trials four times. To begin a trial, 20 prey (per tank) were anesthetized in 50 **mg/L** MS-222 and descaled on both sides of the body using a soft-blade stainless steel spatula to achieve the required scale loss. Fish were returned to the circular tanks for the appropriate recovery period. **Equal** numbers of control fish were placed in the anesthetic, allowed the appropriate recovery period, and received no further disturbance. Following recovery, both groups were rapidly transferred from the recovery tank to the experimental tank. After 24 h, surviving prey were netted from the tanks and identified. Because these experiments were very preliminary, the results will be presented in a qualitative context.

Stressed vs. Unstressed Selection Experiments

Experimental apparatus.-We constructed a rectangular, completely recirculating fiberglass raceway to conduct these

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experiments (Figure 9). Our intentions with this system were to create-a large, flowing water environment in which to conduct experiments. The raceway measures 7.6 m long, 1.2 m wide, and 1.2 m deep; total volume was 11,326 L. Water flow - was produced by a 450 **gal/min** centrifugal pump. The pump intake was a 15 cm diameter port, reduced to flow through 10 cm diameter PVC pipe, and ultimately discharged into the raceway through a 10 cm diameter port. A butterfly valve was installed in the PVC pipe to control flow. Water level was maintained by a standpipe in the downstream end: makeup water was added at approximately 1.0 **L/min.** Water was also passed through a mechanical filter and ultraviolet light sterilizer by a separate pump unit. After leaving the filtration unit, water passed through an electrical heating unit and a cracking column before being discharged into the raceway and a prey holding tank (see below). Lighting, comprised of three 50-W incandescent lights evenly spaced above the raceway, was controlled by a timer to simulate ambient photoperiod. Plexiglas windows covered with nylon screen were inserted at even intervals along the side of the raceway and curtains erected around the perimeter to permit observation without disturbing the fish. An aluminum tank (1.2 m long, 0.7 m wide, 0.6 m deep) was installed at the upstream end above the raceway to hold juvenile salmon prior to predation trials. The tank could be partitioned into two equal size compartments with a removable divider and received raceway water that re-entered the raceway via standpipes. Fish were released into the raceway by removing the standpipes. Screening covered the tank and raceway to prevent fish from jumping out.

To facilitate fish observations, we installed a video system consisting of two cameras, one underwater and the other above the raceway (Figure 9). The underwater camera was mounted on a PVC frame at mid-water level in the downstream end of the raceway. The above tank camera was mounted on rafters above the raceway towards the downstream end. Both cameras
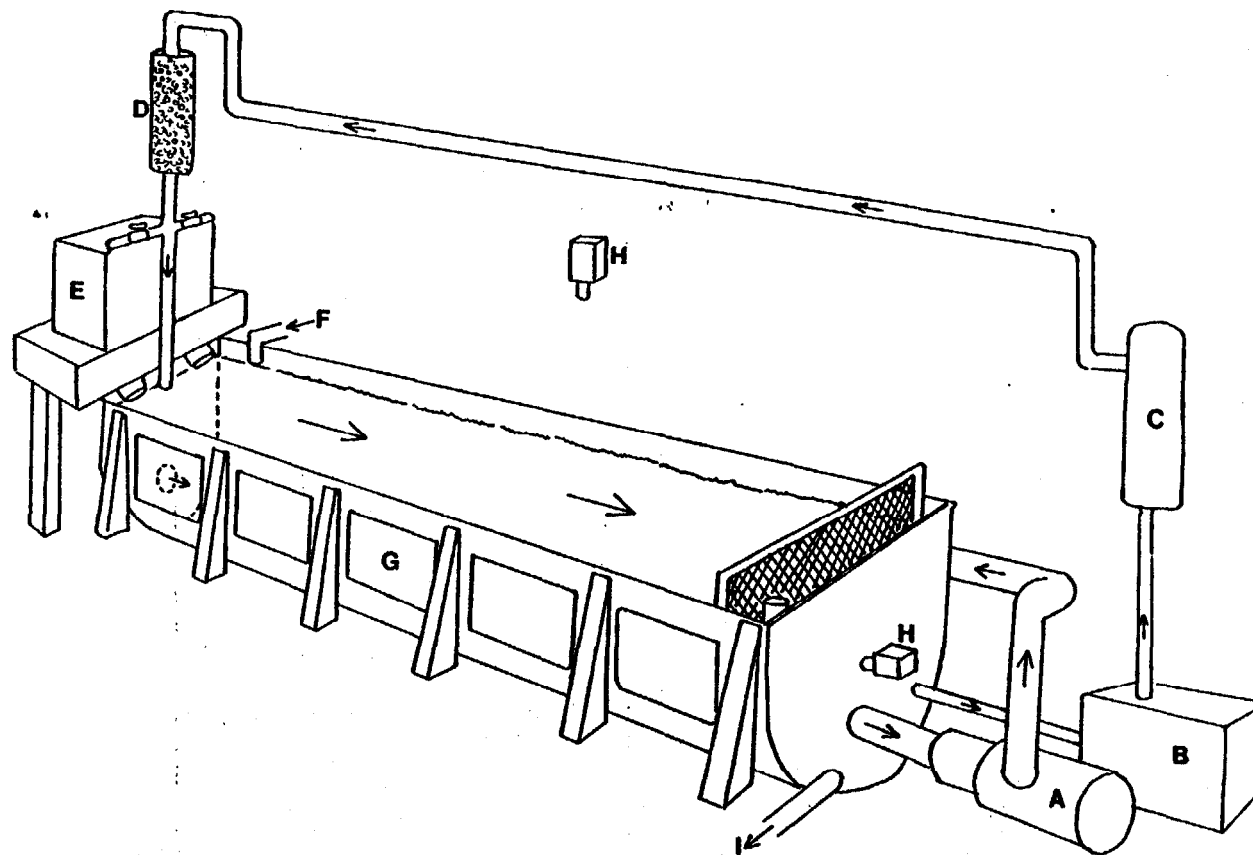
Figure 9. Diagram of the raceway used for selective predation experiments. Arrows indicate direction of water flow. A = recirculation pump; B = filtration unit; C = heater; D = cracking column; E = prey holding tank; F = makeup water inlet; G = Plexiglas window; H = video cameras; I = outflow drain.

could be connected individually to a time lapse video recorder and monitor. To clarify images and estimate northern squawfish reaction distance, we analyzed and image enhanced video tapes using JAVA video analysis software (Jandel Scientific, Corte · **Madera,** California).

Experimental design.-We evaluated the efficacy of the raceway system by conducting a series of preliminary selective predation trials using stressed and unstressed juvenile spring chinook salmon. These trials allowed us to evaluate the conduct of predation experiments in this type of system, assess the relative importance of several variables (e.g. starvation period, experiment duration, etc.), and refine experimental designs for future, more rigorous tests.

Experiments were conducted from August to October, 1989. Prior to all trials, chinook salmon were graded by size, cold branded on either the right or left side, and held separately in 0.6 m diameter, 100 L tanks for at least two weeks to allow recovery. For each trial, 10 northern squawfish were transferred from the circular tanks to the raceway; 50 chinook salmon from each cold branded group were transferred to and held separately in the holding tank. One group of right- or left-branded prey was randomly designated as the treatment (stressed) group; the other group served as controls. All fish were held for at least 1 week to acclimate to the new environs and maintained as described previously. Individual northern squawfish were used for a maximum of two trials.

To begin a trial, predators were starved for 24 h prior to introducing the prey. At 0700 h on the morning following predator starvation, the group of prey designated as treatment fish were subjected to three acute handling stresses separated **by 1 h,** a procedure modified after Barton et al. (1986). Our objective was to use a **stressor** severe enough to elicit physiological stress responses similar to those obtained by Maule et al. (1988) for chinook salmon subjected to the bypass, collection, and handling procedures at **McNary** Dam. The

handling stress consisted of netting the fish out of the
aluminum tank, holding them in the air for 30 s, and returning
them to the tank for recovery. At 0.5 h following the third
stress, 10 fish from each group were netted and immediately   ·
placed in a lethal dose of MS-222 (200 **mg/L)**. The fish were
then removed from the anaesthetic and bled into an ammonium
heparinized capillary tube after severance of the **caudal**
peduncle. Plasma was obtained by centrifugation and stored at
-15°C for future assay of physiological indicators (see below).
Immediately following removal of fish for blood samples, we
removed the tank divider and allowed the remaining control and
treatment fish to mix for 5 min; they were then released into
the raceway by removing the standpipes. Predation was allowed
to proceed for 6 or 24 h (three replicates each); all surviving
prey were netted from the raceway and identified and
enumerated.

We used the depredation ratio (dp: Barns 1967; Coutant 1973)
to assess predator preference:

$$dp = i_t/i_c$$

where i_t and i_c are the instantaneous mortality rates for
treatment and control fish, respectively; i =--log, S, where **S**
is the survival ratio, i.e. the number of fish at the
end/number at start. A dp value of 1 indicates **equal**
susceptibility to predation of treatment and control fish.
Chi-square analysis was used to test for differences in
survival rate between treatment and control groups.

Stress Evaluations

To document the effects of the multiple handling stress
used in the selective predation experiments, we conducted
experiments on chinook salmon to assess the dynamics of plasma
cortisol (a primary physiological indicator of stress) and the

behavioral reaction to a negative stimulus. These experiments
were relevant because the stress response can be extremely
polymorphic due to genetics, rearing history, species, etc. and
would provide objective measures of the severity of the stress.

Physiological experiments.-Fifty juvenile spring chinook
salmon were maintained in each of eight 0.6 m diameter
circular, flow-through tanks receiving 4 **L/min** heated well
water **(12-14°C).** The fish were fed a maintenance diet of
BioMoist feed, held under natural photoperiod, and acclimated
for at least two weeks before experimentation.

Tanks were randomly assigned to one of four treatments:
(1) a single handling; (2) two handlings separated by 1 h; (3)
three handlings, each 1 h apart: or (4) undisturbed controls.
This design resulted in two replicate tanks per treatment. The
handling stress was as described previously. Blood samples
were collected from 5 fish just before each stress, and at 0.5,
1, 3, 6, 12, 24, and 168 h after the final stress.   The
experiment was conducted on August 7-8, 1989.

Plasma was obtained and stored as previously described.
Plasma cortisol was determined by ^{3}**H-radioimmunoassay** (Foster
and Dunn **1974),** as modified by **Redding** et al. (1984) for use
with **salmonid** plasma. All data were tested for homogeneity of
variance (Bartlett's test, Sokal and Rholf 1981). Those found
to be homogenous were treated **by** analysis of variance followed
by Fisher's Least Significant Difference Test at the 5%
probability level (Ott 1977). Data with heterogeneity among
the means were either transformed to stabilize the variance or
subjected to a **Kruskal-Wallis** One-Way Analysis by Ranks (Sokal
and Rholf 1981).

Behavioral **experiments.-As** a behavioral indicator of the
effects of stress, we determined the response times for
individual fish by exposing them to a sudden, continuous light
and measuring the time it took for each fish to swim to cover,
as in the protocol of Sigismondi and Weber (1988). Juvenile
spring chinook salmon used in these experiments were maintained

as described for the physiological experiments. Behavioral experiments were carried out in two "**Living** Stream" systems (Frigid Units, Inc., Toledo, Ohio) each 2.13 m long, 0.60 m wide, and 0.56 m deep. Water was completely recirculated by an electric pump, maintained at **10-12°C** by a cooling unit, and passed through a two-stage filtering system.   Divider screens were used to partition the tank into one large (1.1 m x 0.6 m) and one small (0.5 m x 0.6 m) compartment. Fitted over the large compartment was a permanent black plastic cover mounted on a wooden frame; the cover extended 0.45 m from a screen shielding the pump and then angled **(90°)** down into the water before stopping approximately 10 cm from the bottom. A 75-W incandescent light was positioned 40 cm above the small compartment. The small compartment, and the remaining open area of the large compartment, were fitted with a removable black plastic sheet mounted on a wooden frame.

Fish were exposed to one of three treatments: (1) three handling stresses separated by l-h: (2) an agitation stress; and (3) undisturbed controls. The agitation stress consisted of filling a 19 L bucket approximately **1/3** full with water, netting fish from the experimental tank to the bucket, and pouring the fish into another bucket located on the floor: water fell a distance of about 1.0 m. The buckets were then switched and the process continued for 4 min before returning the fish back to the experimental tank. The behavioral response was then measured immediately or after a 1, 3, 6, or 24 h recovery period. The treatments were randomly assigned to consecutive days, with tanks serving as replicates on any given day.

To conduct a test, six fish were introduced into the small compartment of each tank and allowed to adjust overnight. The lights were off and covers in place. The next morning, all fish (except controls) were rapidly netted out of the tank and subjected to either the handling stress or the agitation stress. After the stress, fish were returned to the small

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compartment and the cover replaced until the next stress or
until the appropriate recovery time had elapsed. After the
recovery period, the cover was removed while simultaneously
removing the divider screen and switching on the light. We   ·
switched off the pump/chiller unit 0.5 h before application of
the stimulus to reduce disturbance to the fish. The time taken
for each fish to swim under the permanent cover was recorded
using an event recorder. A test ended when the last fish
reached cover or after 30 min, whichever came first. General
notes on the behavior of the fish were also recorded, such as
whether fish moved in and out of cover and their degree of
excitability. On each day, the initial stress was applied at
0800 h for fish in one tank and 0.5 h later in the second tank;
data from the six fish in each replicate tank were pooled for
analysis.

   The median response time was calculated for each pooled
sample because the data were not distributed normally. Within
each recovery period, we used a nonparametric **Kruskal-Wallis**
test to determine whether the medians differed among the
treatment groups. When medians differed significantly, a
nonparametric Tukey-type multiple comparison procedure was used
to determine where differences actually existed (Zar 1984).

                               Results

   Although we present some results in a statistical context,
we considered the use of statistics only another part of
developing protocols. We reiterate that the results should be
considered preliminary and caution readers to interpret them as
such.

   <u>Live vs. Dead **Experiments.-Northern**</u> sguawfish consumed
significantly more dead than live chinook salmon (z = 6.28, **P** <
0.001). Overall, 65% of the prey consumed were dead. In only
4 of 18 replicates were live prey consumed at a higher
frequency than dead prey (Figure 10). Dead prey typically sank
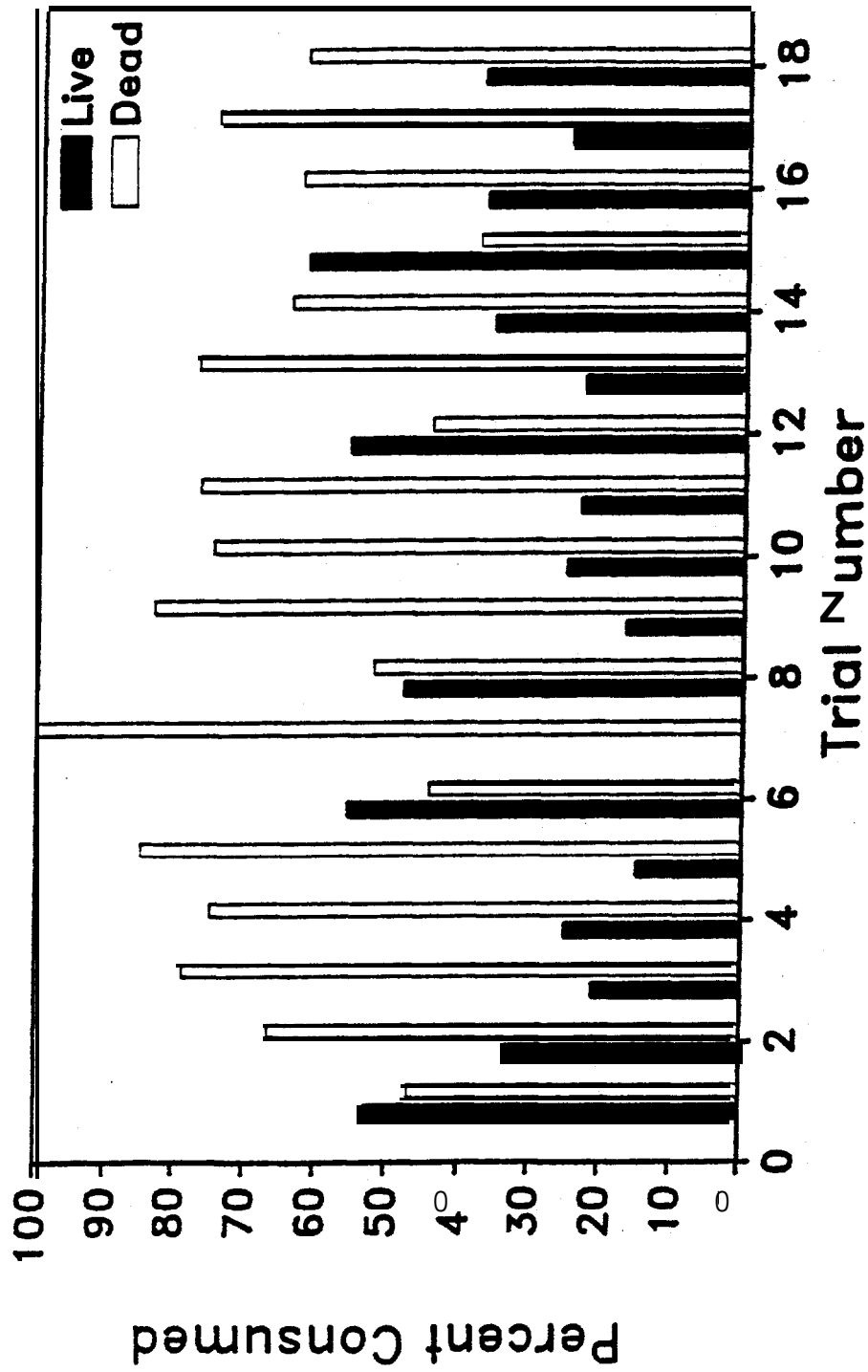
Figure 10. Percent of live or dead spring chinook salmon consumed by northern squawfish during selection experiments. Bars are the values for 18 replicates.

to the bottom of the tank within 1 min of release.

Injured vs. Non-injured Experiments.-In all trials, northern squawfish consumed more descaled than non-descaled chinook salmon (Table 10). Overall, > 80% of all prey consumed were descaled. During all trials, there was a high rate of regurgitation (Table 10), with more descaled fish regurgitated than controls. Of all prey attacked and ingested, almost 60% were regurgitated.

Stressed vs. Unstressed Experiments.-There was little evidence for northern squawfish selection of either stressed or unstressed prey, regardless of experiment duration. For both the 6 and 24 h experiments, the survival rate of stressed and control prey did not differ (6 h: x^2 = 1.275, P > 0.05; 24 h: x^2 = 0.6976, P > 0.05). The depredation ratios of fish in the 6 and 24 h experiments were 1.075 and 0.949, respectively, indicating that both stressed and control groups were equally susceptible to predation. Plasma cortisol in stressed fish was significantly higher than controls for all trials (Figure 11).

Physiological experiments.-Plasma cortisol responded in a cumulative manner with each application of an additional acute disturbance (Figure 12). For all groups, cortisol peaked at 0.5 h after the final stress and returned to control levels by 6 h.

Behavioral experiments.-The median response times of stressed fish were significantly greater than those of controls immediately after the stress and at 1 and 6 h post stress (Figure 13). Control fish typically darted to cover within 10 s. Fish receiving the agitation stress showed the longest response time immediately after the stress but responded similarly to controls for other recovery periods. The response times in fish receiving the handling stresses showed a somewhat inconsistent pattern, being high at 0, 1, and 6 h and low at 3 and 24 h after the final stress. Response times of all fish were highly variable, as indicated by the range of times for each group (Table 11).
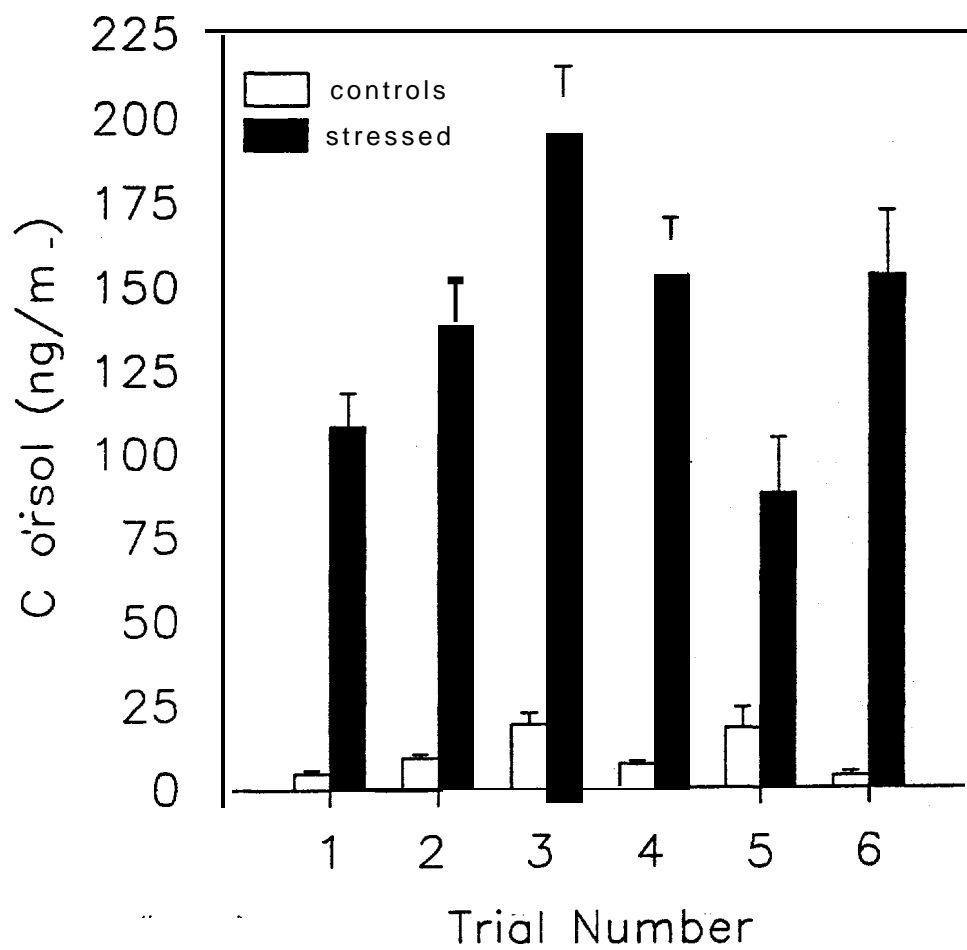
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Figure 11. Mean (and SE) plasma cortisol titers of juvenile spring chinook salmon (N = 10) subjected to three 30-s handling stresses separated by 1 h relative to unstressed controls prior to being exposed to predation.

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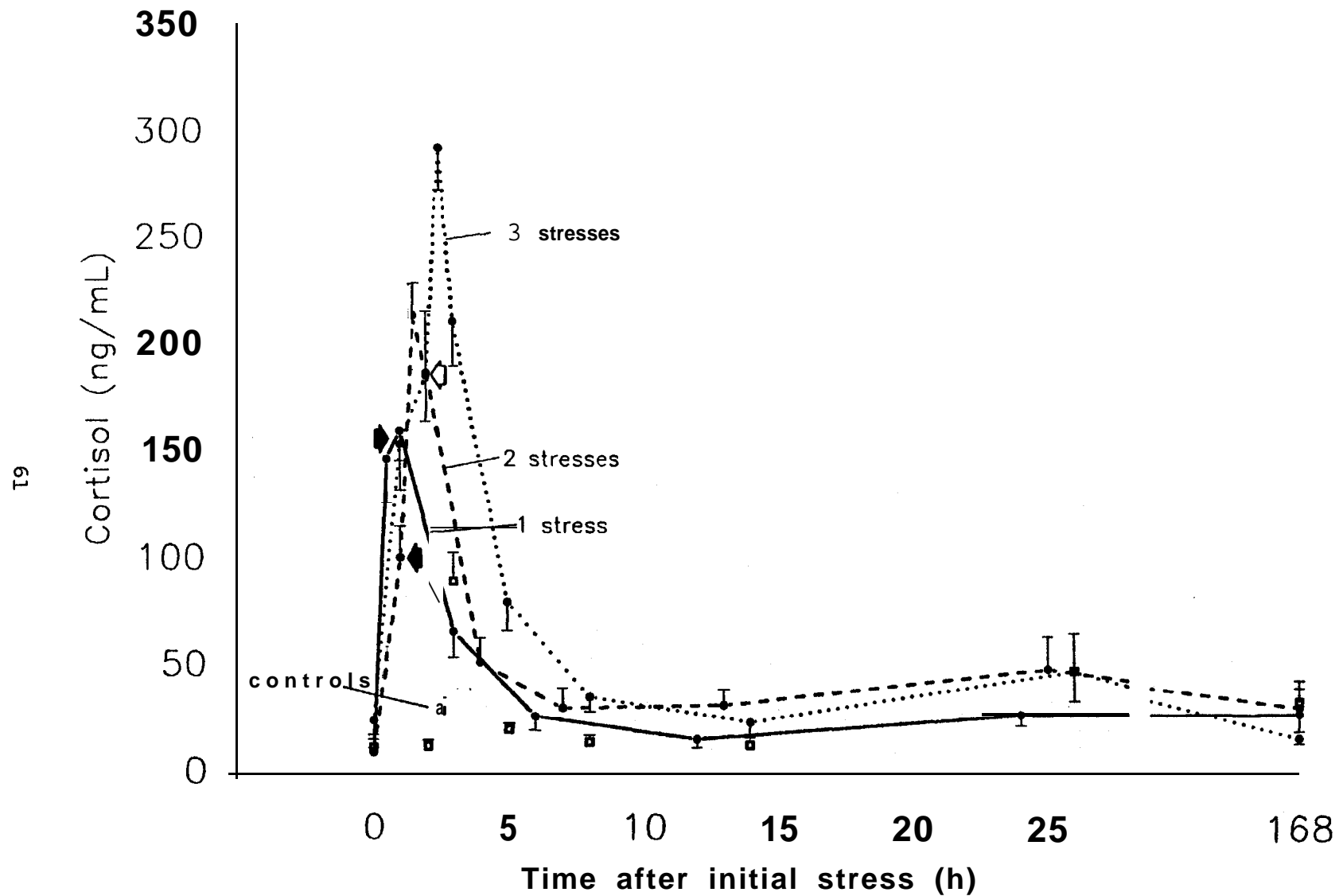
Figure 12. Mean (and SE) plasma cortisol dynamics of juvenile spring chinook salmon (N = 10) subjected to either one, two, or three 30-s handling stresses separated by 1 h. Solid arrows indicate application of the second stress and the open arrow indicates application of the third;

Figure 13. Median response times to swim to cover after exposure to a continuous bright light for juvenile spring chinook salmon subjected to three 30-s handling stresses separated by 1 h, an agitation stress, or unstressed contols.
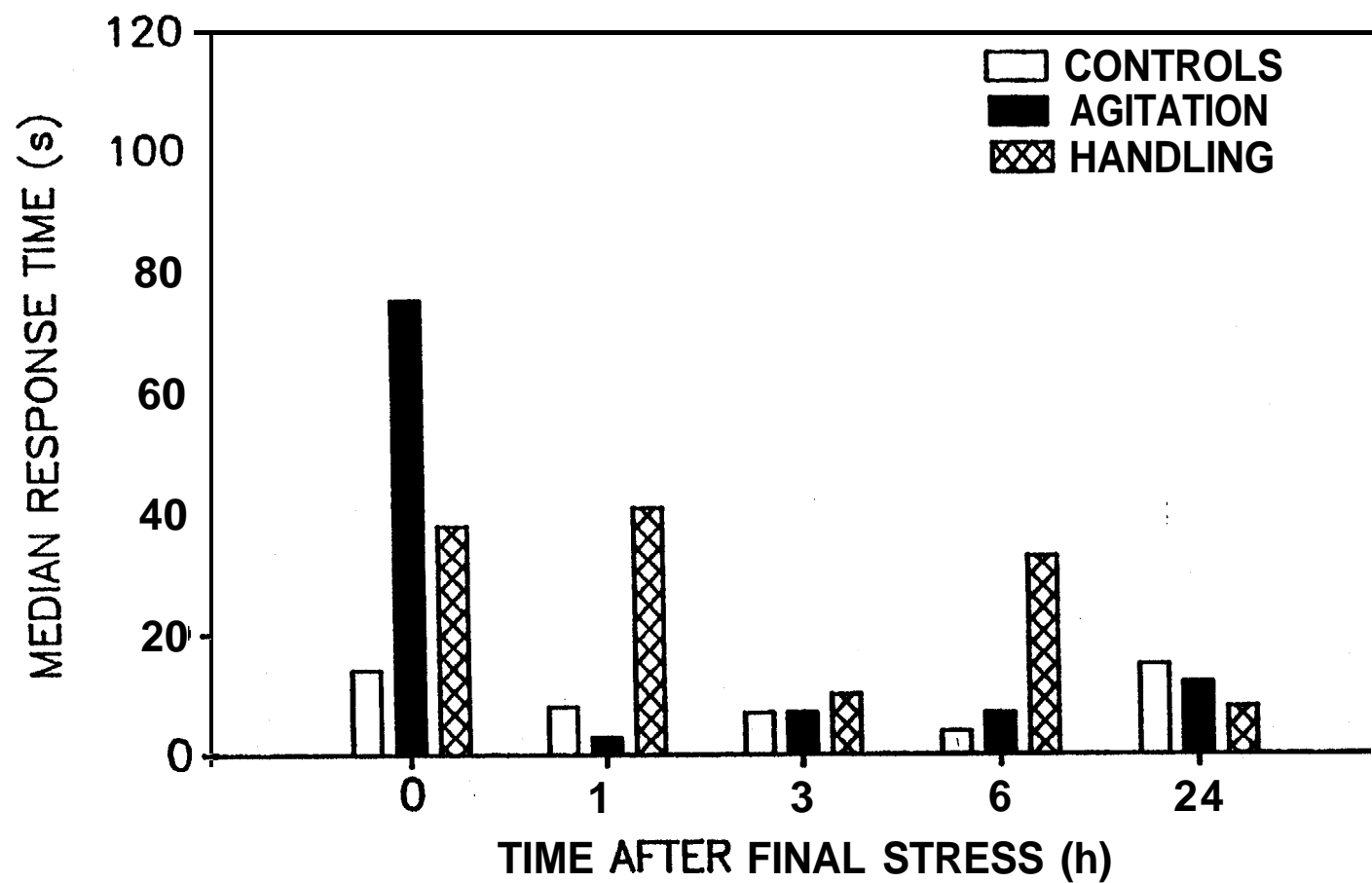
Table 10. The number of prey available, eaten, and regurgitated in selective predation experiments using descaled and non-descaled prey. Data are from all replicates of an experiment combined. DSC = descaled fish: CON = controls.

	Prey					
Experiment description	Available		Eaten		Regurgitated	
	DSC	CON	DSC	CON	DSC	CON
50% descale 24 h recov.	60	60	8	0	17	0
50% descale 1 h recov.	60	60	13	2	14	2
20% descale 1 h recov.	60	60	10	1	7	4

Table 11. Range of times (s) for juvenile spring chinook salmon to swim to cover after exposure to a sudden bright light for fish subjected to an agitation stress, three handling stresses, or unstressed controls. Recovery time is the time (h) allowed after application of the stress before testing.

Recovery Time (h)	Response Time (s)		
	Controls	Agitation Stress	Handling Stress
0	0.4-35.7	7.5-1070.8	2.6-140.8
1	2.3-331.9	0.3-327.5	2.4-682.2
3	0.4-182.8	0.2-568.1	1.0-38.6
6	0.4-41.7	0.2-1535.1	0.4-167.1
24	3.3-679.2	5.6-237.0	1.4-90.4

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Upon exposure to the light, control fish were typically very excited and swam erratically around the tank before seeking cover. It was common, however, for stressed fish to remain motionless or swim slowly on the bottom. When stressed fish finally sought cover, they typically did so in a smoother, less erratic fashion. Several fish in all groups repeatedly darted in and out of cover.

Discussion

The primary objective of this work was to develop the laboratory and field protocols necessary to evaluate selective predation and prey vulnerability. The laboratory we used for live vs. dead and injured vs. non-injured selection experiments has been in use since 1985 (Lucchetti and Gray 1988). Several key attributes were addressed in the design of this laboratory, including disease control, water **quality,** temperature control, and efficiency and ease of operation. Lucchetti and Gray (1988) successfully held northern squawfish for up to 6 months with no disease or water quality problems and Beyer et al. (1988) conducted northern squawfish consumption rate experiments in this laboratory. Because of the history of this wet laboratory, little modification was necessary and we believe it worked well in allowing us to evaluate selective predation under the simplest of conditions.

Our results revealed that northern squawfish preferred dead over live prey by almost a 2 : 1 ratio. In contrast, Irvine and Northcote (1983) found that underyearling rainbow trout Oncorhvnchus mvkiss preferred live over dead prey and concluded that body movement was an important prey characteristic to stream rearing trout. Also, **Howick** and O'Brien (1983) noted that prey movement increased reaction distance and probability of attack in largemouth bass **Micropterus salmoides.** We believe our results may provide some insight into the functional role of northern squawfish as a predator. If, for example, northern

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sguawfish prefer dead over live prey, these fish may be more of a scavenger than an active predator. This information would question the overall impact northern sguawfish have as predators on juvenile salmonids. Assuming that food quality · (Krebs and Davies 1978) of live and dead prey are similar, selecting dead prey may be energetically most efficient. As Stein (1977) points out, predators should minimize costs associated with locating, pursuing, capturing, and ingesting prey while maximizing benefits from prey consumption in terms of energy gained. Of course, more research is needed to determine whether this situation occurs in the natural environment.

Our results suggested that descaled prey were more vulnerable to predation than non-descaled prey. Scales are usually lost when smolts are trapped and transported around dams or when they pass through turbines and spillways. The importance of the integument complex in maintaining ionic and osmotic balance is well known (Van Oosten 1957) and the effects of descaling on fish mortality have received much attention. Kostecki et al. (1987) noted that scale loss was greater in Atlantic salmon Salmo salar that had died within 48 h after passage through a turbine than in fish that survived longer or controls. Gloss and Wahl (1983), assessing the mortality incurred by migrating Atlantic salmon passing through turbines, found a significant relationship between fish size and mortality. Bouck and Smith (1979) found that experimental removal of 25% of slime and scales from coho salmon caused no deaths in fresh water but 75% mortality within 10 d in sea water. In this study, we held 27 fish that had been descaled 20% to evaluate delayed mortality. Within 2 h, 5 fish had died and others were showing abnormal swimming behavior. Within 24 h, 44% of the fish had died and some abnormal swimming behavior was still present. The results of these studies suggest that descaling per se may contribute little to mortality and that physical trauma may be more important, as stated by Kostecki et

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al. (1987). It is possible that short term behavioral and physiological effects of descaling and physical trauma may affect the performance of juvenile salmon, thereby rendering them more vulnerable to predation. More research is needed to fully evaluate this hypothesis.

We constructed the raceway tank to create a larger, more realistic environment in which to conduct selection experiments. Several investigators have used large, flowing systems to study the ecology and behavior of stream fish (Mason and Chapman 1965; Reeves et al. 1983; **Fausch** and White 1983; Congleton et al. 1985). From an operational standpoint, we encountered few problems and the system was virtually maintenance free. Water velocity varied throughout the length of the raceway (Table 12) with a turbulent surface flow created in the most upstream 2.5 m and flow smoothing out further downstream. Because of the single discharge port, two large back eddy areas were created that provided refuge for both northern **squawfish** and juvenile salmon. Some improvements to be made in the future would include developing an easier way to collect fish out of the raceway, producing more uniform, laminar flow, and using screens to partition the tank into smaller areas.

We encountered several problems with our video system which must be solved if video is to be used for behavior observations. Although several investigators have successfully used video as an aid in the study of fish behavior (Rand and Lauder 1981; Webb 1984a; Blaxter and **Batty 1987;** Lawrence and Smith **1989),** such filming was often done using small aquaria where the logistical difficulties **were** reduced. The sheer size of the raceway created field of view problems for both the overhead and underwater cameras. The overhead camera field of view covers only a small fraction of the length of the raceway: wide angle lenses or multiple cameras could be

Table 12. Water velocities at selected distances from the
upstream end of the fiberglass raceway used for selective
predation experiments.   Surface, mid, and bottom refer to the
position in the water column where the measurement was taken.

		Water velocity (cm/s)		
Distance (m)		Surface	Mid	Bottom
Upstream	1	12.2	73.2	18.3
	2	15.2	67.1	36.6
	3	21.3	42.7	18:3
	4	9.1.	6.1	12.2
	5	15.2	9.1	3.1
	6	6.1	3.1	6.1
Downstream	7	9.1	6.1	9.1

used to overcome this problem.   It was common for predator-
prey interactions to occur very close to the underwater camera
and out of the field of view, thereby precluding them from
being recorded on tape.   Recent work in the raceway has shown
that partitioning off the area around the camera and using
brighter lights provided underwater videotape of much better
quality.   Water turbulence and surface glare were additional
difficulties to overhead filming.   Blaxter and Batty (1985)
used a raft of transparent Perspex set at an angle to eliminate
light reflection during overhead filming; it is possible that a
modification of that method could reduce turbulence and glare
in the raceway.   Perhaps the largest filming obstacle to be
overcome is the ability to film in the dark.   Although infra-
red-sensitive TV cameras have been used successfully to study
fish behavior in the dark (Blaxter and Batty 1985, 1987), the
filming was done over relatively small areas.   Our preliminary

experiments in the raceway indicated that much of the feeding activity of northern sguawfish occurred at night. Indeed, Congleton et al. (1985) were unable to observe northern sguawfish behavior in feeding experiments due to the nocturnal activity of the fish. Clearly, a more thorough understanding. of northern sguawfish behavior may be possible if we can solve the problems involved with filming in the dark.

Although northern sguawfish did not show selection for stressed prey, conclusions based on this would be premature because these experiments have not been fully completed. Our intentions in conducting these experiments were to learn about the operation of the raceway, evaluate and manipulate important variables, observe fish behavior, and refine experimental designs; generating rigorous data from these experiments was of secondary importance. We used multiple acute handling stresses to produce a stress response similar to that obtained by Maule et al. (1988) for fish passing through the collection system at **McNary** Dam. Maule et al. (1988) noted three characteristics of the collection system: the system was stressful, the stresses were acute, and each element of the collection system had cumulative effects on the fish. Our multiple stress protocol could be described in a similar manner. Our peak cortisol values were similar to those obtained by Maule et al. (1988) and lower than those for fall chinook salmon used by Barton et al. (1986). One major difference in the three studies was recovery dynamics--our fish required 6 h for cortisol to return to control levels versus a recovery period of 12-48 h for fish used by Maule et al. (1988) and Barton et al. (1986). We believe that our multiple stress protocol, although physiologically disturbing to the fish, was probably missing some stressful elements that contribute to changes in prey vulnerability, notably physical trauma, disorientation, and fatigue. Future research will attempt to address this question.

The effects of stress on fish become apparent as sublethal

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changes in a variety of blood constituents (see Mazeaud et al.
1977 and Schreck 1981 for reviews) and as general lethargic
behavior (Bouck and Ball 1966; Sigismondi and Weber 1988).
Sigismondi and Weber (1988) stated that a likely consequence of
these effects is increased exposure and vulnerability to
predation.   Indeed, several investigators have found that
exposure to temperature shock or contaminants increased the
vulnerability of prey to predators (Hatfield and Anderson 1972;
Coutant 1973; Coutant et al. 1974).   Olla and Davis (1989)
found that coho salmon stressed by 60 s of handling showed a
decreased ability to avoid predators, but recovered from this
effect in 90 min.   Congleton et al. (1985) reported that
vulnerability to rainbow trout and northern squawfish predation
increased in several stocks of spring chinook salmon subjected
to chronic crowding stresses.

     The lack of northern squawfish selection for stressed prey
may have been due to complications in experimental design and
behavior of the juvenile salmon.   For example, when predation
was allowed to proceed for 24 h, almost all prey were eaten and
the effects of stress were probably much reduced as time
elapsed.   Reductions in prey availability and consumption of
all prey are important considerations in selectivity
experiments (Bans 1967; Coutant et al. 1974).   A more
complicated problem, however, was the schooling behavior of the
juvenile salmon.   Just after release, salmon were scattered
randomly throughout the raceway.   After predator attacks
started, most salmon would group together, move to the top of
the water column, and remain tightly schooled.   The advantages
of schooling fish in countering predators has been well
documented (see Pitcher 1986 for a recent discussion). We
believe that stressed fish gained benefits from the school,
even though on an individual basis performance capacity (sensu
Schreck 1981) may be reduced; the end result is apparent random
feeding by northern squawfish.   Changes in experimental design,
such as introducing groups separately or using shorter

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experiment durations, may clarify selective predation on stressed fish and should provide needed insight into the relative vulnerability of stressed fish to predation.

Results of both the physiological and behavioral tests   -
indicate that treatment fish exposed to predation were stressed. In the behavioral response test, although we adapted our procedures after Sigismondi and Weber **(1988),** the results were clearly different. Sigismondi and Weber (1988) reported median response times commonly > 1 min and ranges that often spanned to 30 + min; we rarely achieved response times > 1 min and our ranges were much smaller. There are several possible explanations for these discrepancies, including use of different strains and sizes of fish, different experimental systems, and our handling stresses separated by 1 h instead of 3 h. Nevertheless, we agree with the conclusion of Sigismondi and Weber (1988) that likely consequences of a large response time latency and lethargic behavior are increased vulnerability to predation or other environmental hazards. Given that predators attack using acceleration fast-starts that take < 1 s (Webb 1976, **1984b),** even slight changes in behavior could adversely affect fish survival.

We believe our laboratory experiments have provided some interesting results to test in the field, although the results should be considered preliminary and some experiments are not yet fully complete. The advantages of laboratory experiments are relative simplicity, and the ability to manipulate important variables and have adequate replication. Although the realism of laboratory experiments has often been questioned, Diamond (1986) noted that in some instances, particularly physiological or behavioral ecology, laboratory experiments can be quite realistic. We believe our results demonstrated that we have the facilities and experimental designs necessary to perform selective predation and prey vulnerability experiments. Future experiments will be aimed at a more rigorous evaluation of selective feeding of northern

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squawfish, both in the laboratory and field, and evaluating how
stress, injury, etc. might affect the relative vulnerability of
juvenile salmon to predation.

LITERATURE CITED

Adams, S. M. and D. L. **DeAngelis.** 1987. Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. In: Predation: Direct and Indirect Impacts on Aquatic Communities. W. C. Kerfoot and A. Sih (eds). University Press of New England, Hanover, NJ.

Allen, J.D., A.S. **Flecker,** and N.L. **McClintock.** 1987. Prey preference of stoneflies: sedentary vs. mobile prey. Oikos **49:323-331.**

Amundsen, P. and A. Klemetsen. 1986. Within-sample variabilities in stomach **contens** wight of fish - implications for field studies of consumption rate. In: Contemporary Studies in Fish Feeding: the Proceedings of **gutshop '84.** Developments in Environmental Biology of Fishes 7. (C. A. Simenstat and G. M. Caillet, eds.). pp. 307-314. Boston, Dr. W. Junk.

Anderson, R. M. 1965. Methods of collecting and preserving vertebrate animals. Bulletin No. 69, National Museum of Canada.

Anonymous. 1987. Columbia Basin Fish and Wildlife Program. Northwest Power Planning Council, Portland, Orgeon. 246 p.

Bajkov, A. D. 1935. How to estimate the daily food consumption of fish under natural conditions. Trans. Am. Fish. **Soc. 65:288-289.**

Bans, R. A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Bd. Canada **24:1117-1153.**

Bartell, S. M., J. E. **Breck,** R. H. Gardner, and A. L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. Can. J. Fish. **Aquat.** Sci. **43:160-168.**

Barton, B.A., C.B. Schreck and L.A. Sigismondi. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile chinook salmon. Trans. Am. Fish. **Soc. 115:245-251.**

Basu, S. P. 1959. Active respiration of fish in relation to ambient concentrations of oxygen and carbon dioxide. J. Fish. Res. Bd. Canada. **16:175-212.**

Beamesderfer, R. C., R. E. Rieman, J. C. Elliott, A. A. Nigro and D. L. Ward. 1987. Distribution, abundance and population dynamics of northern sguawfish, walleye, smallmouth bass, and channel catfish in John Day Reservoir, 1986. Annual Progress Report. Bonneville Power Administration, Portland, OR.

Beamesderfer, R. C. and B. E. Rieman. 1988. Predation by resident fish on juvenile salmonids in a **mainstem** Columbia Reservoir: Part III. Abundance and distribution of northern sguawfish, walleye, and smallmouth bass. In: Poe, T. P. and B. E. Rieman **(eds.),** 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts **DE-A179-82BP34796** and **DE-A179-82BP35097)** Bonneville Power Administration, Portland, OR.

Beamesderfer, R. C., B. E. Rieman and S. Vigg. 1988. Simulation of predation by a resident fish on juvenile salmonids in a Columbia River reservoir. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts **DE-A179-82BP34796** and **DE-A179-82BP35097)** Bonneville Power Administration, Portland, OR.

Beyer, J. M., G. Lucchetti, and G. Gray. 1988. Digestive tract evacuation in northern sguawfish (<u>Ptychocheilus oreaonensis</u>). Can. J. Fish. Aguat. Sci. **45:548-553.**

Black, E. C. 1953. Upper lethal temperature of some British Columbia freshwater fish. J. Fish. Res. Bd. Can. 10:196-210. [Cited by Xi He, unpublished MS].

Blaxter, J.H.S., and R.S. Batty. 1985. Herring behaviour in the dark: responses to stationary **and continuously** vibrating obstacles. J. Mar. Biol. Ass. U.K. **65:1031-1049.**

Blaxter, J.H.S., and R.S. Batty. 1987. Comparisons of herring behaviour in the light and dark: changes in activity and responses to sound. J. Mar. Biol. Ass. U. K. **67:849-860.**

Boisclair, D. and W. C. Leggett. 1988. An in situ experimental evaluation of the Elliott and Persson and the Eggers models for estimating fish daily ration. Can. J. Fish. Aguat. Sci. **45:138-145.**

Bouck, G.R. and R.C. Ball. 1966. Influence of capture methods on blood characteristics and mortality in the Rainbow Trout (<u>Salmo aairdneri</u>). Trans. Am. Fish. **Soc. 95(2):170-176.**

Bouck, G. R. and S. D. Smith. 1979. Mortality of experimentally descaled smolts of **coho** salmon (Oncorhynchus kisutch) in fresh and salt water. Trans. Am. Fish. **Soc. 108:67-69.**

Carline, R. F. 1987. Simplified method based on bioenergetics modeling to estimate food consumption by largemouth bass and northern pike. Trans. Am. Fish. **Soc. 116:224-231.**

Cech, J. J., Jr., S. J. Mitchell, D. T. Castleberry, and M. McEnroe. 1990 (In Press). Distribution of California stream fishes: influence of environmnental temperature and hypoxia. Environ. Biol. Fish.

Chesson, J. 1978. Measuring preference in selective predation. Ecology **59:211-215.**

Congleton, J.L., T.C. Bjornn, B.H. Burton, B.D. Watson, **J.I,** Irving, R.R. Ringe. 1985. Effects of handling and crowding on the stress response and viability of chinook salmon parr and smolts. Completion Report to Bonneville Power Administration, Portland, Oregon, (contract number **DE-AC79-83BP11196).**

Coutant, C. 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. J. Fish. Res. Bd. Can.. **30:965-973.**

Coutant, C.C., H.M. Ducharme Jr. and J.R. Fisher. 1974. Effects of cold shock on vulnerability of juvenile channel catfish (Ictalurus punctatus) and largemouth bass (Micronterus salmoides) to predation. J. Fish. Res. Bd. Can.. 31: 351-354.

Cui, Y. and R. J. Wootton. 1989. Bioenergetics of growth of a cyprinid, Phoxinus phoxinus (L.): development and testing of a growth model. J. Fish Biol. **34:47-64.**

Cummins, K. W. and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological **energetics.** International Association of Theoretical and Applied Limnology, No. 18:1-158, Stuttgart, Germany.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 **in** Diamond, J. and T.J. Case, eds. Community Ecology. Harper and Row Publishers, New York.

Efron, B. 1982. The Jackknife, the Bootstrap and Other Resampling Plans. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania. No. 38.

Efron, B. and R. Tibshirani, 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Statistical Science, **1:54-77.**

Eggers, D. M. 1979. Comments on some recent methods for estimating food consumption by fish. J. Fish. Res. Bd. Can. **36:1018-1019.**

Elliott, J. M. and L. Persson. 1978. The estimation of daily rates of food consumption for fish. J. Animal Ecol. 47:977-991.

Espinosa, F.A. Jr. and J.E. Deacon. 1973. The preference of largemouth bass (<u>Microoterus salmoides</u> Lacepede) for selected bait species under experimental conditions. Trans. Am. Fish. **Soc. 103:355-362.**

Fausch, K.D., and R.J. White. 1983. Sinuous stream aquarium to simulate **lotic** fish habitat. Prog. Fish-Cult. **45:113-116.**

Fickeisen, D. H., D. D. Dauble, and D. A. Neitzel. 1990. Proceedings of the predator-prey modeling workshop, Friday Harbor, Washington, May 16-19, 1989. Final contract **(DE-AC06-76RLO-1830)** completion report to Bonneville Power Administration, Portland, Oregon.

Fish Passage Center. 1988. Weekly Reports.

Foster, L.B., and R.T. Dunn. 1974. Single-antibody technique for radioimmunoassay of cortisol in unextracted serum or plasma. Clinical Chemistry 20: 365-368.

Gloss, S. P. and J. R. Wahl. 1983. Mortality of juvenile salmonids passing through Ossberger crossflow turbines at samll-scale hydroelectric sites. Trans. Am. Fish. **Soc. 112:194-200.**

Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Trans. Am. Fish. **Soc. 117:55-62.**

Hargreaves, N.B., and R.J. **LeBrasseur.** 1985. Species selective predation on juvenile pink <u>(Oncorhynchus **gorbuscha**)</u> and chum salmon (<u>O. keta</u>) by **coho** salmon **(<u>O.</u>** <u>kisutch</u>). Can. J. Fish. **Aquat.** Sci.s **42:659-668.**

Hatfield, C.T., and J.M. Anderson. 1972. Effects of two insecticides on the vulnerability of Atlantic salmon (<u>Salmo salar</u>) parr to brook trout (<u>Salvelinus fontinalis</u>) predation. J. Fish. Res. Bd. Can. **29:27-29.**

Henchman, T. R. 1986. Distribution and food habits of northern sguawfish, Ptvchocheilus *oreqonensis* (Richardson), and estimates of their consumption of migrating juvenile salmonids in John Day Reservoir and **tailrace** during the spring and summer, 1983. MS Thesis, University of Washington, Seattle.

Hewett, S. W. 1989. Ecological applications of bioenergetics models. American Fisheries Society Symposium, **6:113-120.**

Hewett, S. W. and B. L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute, Report No. **WIS**-SG-87-245.

Hewett, S. W. and B. L. Johnson. 1989. A general bioenergetics model for fishes. American Fisheries Society Symposium, **6:206-208.**

Howick, G.L., and W.J. O'Brien. 1983. Piscivorous feeding behavior of largemouth bass: an experimental analysis. Trans. Am. Fish. **Soc. 112:508-516.**

Irvine, J.R., and T.G. Northcote. 1983. Selection by young rainbow trout (Salmo **gairdneri)** in simulated stream environments for live and dead prey of different sizes. Can. J. Fish. Aguat. Sci. **40:1745-1749.**

Jeppson, P. W. and W. S. Platts. 1959. Ecology and control of the Columbia sguawfish in northern Idaho lakes. Trans. Am. Fish. **Soc. 88:197-202.**

Kitchell, J. F. and J. E. **Breck.** 1980. Bioenergetics model anf foraging hypothesis for sea lamprey (Petromvzon marinus). Can. J. Fish. Aguat. Sci. **37:2159-2168.**

Kitchell, J. F., D. J. Stewart and D. Weininger. 1977. Applications of a bioenergetics model to Yellow Perch (**Perca** flavenscens) and Walleye (Stizostedion vitreum vitreum). J. Fish. Res. Bd. Can. **34:1922-1935.**

Koski, C. H., S. W. **Pettit** and J. L. **McKern,** 1989. Fish Transportation Oversight Team Annual Report-FY 1988 ; Transport Operations on the Snake and Columbia Rivers. NOM Technical Memorandum NMFS **F/NWR-25.**

Kostecki, P. T., P. Clifford, S. P. Gloss and J. C. Carlisle. 1987. Scale loss and survival in smolts of Atlantic salmon (Salmo salar) after turbine passage. Can. J. Fish. Aguat. Sci. 44: 210-214.

Krebs, J.R., and N.B. Davies. 1978. Behavioural ecology an evolutionary approach. Sinauer Associates, Inc. Sunderland, Massachusetts.

Lawrence, B.J., and R.J.F. Smith. 1989. Behavioral responses of solitary fathead minnows, _Pimphales promelas_, to alarm substance. J. Chem. Ecol. **15:209-219.**

Lucchetti, G.L., and G.A. Gray. 1988. Ptototype water reuse system. Prog. Fish Cult. **50:46-49.**

Mason, J.C., and D.W. Chapman. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile **coho** salmon in stream channels. J. Fish. Res. Bd. Can. **22:173-190.**

Maule, A.G., C.B. Schreck, C.S. Bradford, and B.A. Barton. 1988. Physiological effects of collecting and transporting emigrating juvenile chinook salmon past dams on the Columbia River. Trans. Am. Fish. **Soc.** 117: 245-261.

Mazeaud, M.M., F. Mazeaud, and E.M. Donaldson. 1977. Primary and secondary effects of stress in fish: some new data with a general review. Trans. Am. Fish. **Soc. 106:201-212.**

Nigro, A. A., S. Vigg and C. Burley. 1990. Development of a system-wide predator control program: **Stepwise** implementation of a predation index, predator control fisheries, and evaluation plan in the Columbia River Basin. Annual Progress Report, August 1988 - September 1989, Project Summary. Project Number 82-028, Bonneville Power Administration.

Olla, B.L., and M.W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared **coho** salmon (_Oncorhvnchus kisutch_) juveniles. Aguaculture **76:209-214.**

Olson, R. J. and A. J. Mullen. 1986. Recent developments for making gastric evacuation and daily ration determinations. Environ. Biol. Fishes **16:183-191.**

Ott, L. 1977. An introduction to statistical methods and data analysis. Duxbury Press, North **Scituate,** Massachusetts.

Pennington, M. 1985. Estimating the average food consumption by fish in the field from stomach contents data. Dana 5:81-86.

Pitcher, T.J. 1986. Functions of shoaling behaviour in teleosts. Pages 294-337 In: T.J. Pitcher, ed. The Behaviour of Teleost Fishes. The Johns Hopkins University Press, Baltimore, MD.

Poe, T. P., H. C. Hansel, S. C. Vigg, D. E. Palmer and L. A. Prendergast. 1988. Predation by resident fish on juvenile salmonids in a **mainstem** Columbia River Reservoir: Part I. Feeding ecology during the **salmonid** out-migration. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts **DE-A179-82BP34796** and **DE-A179-82BP35097)** Bonneville Power Administration, Portland, OR.

Poe, T. P. and B. E. Rieman (eds.). 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts **DE-A179-82BP34796** and **DE-A179-82BP35097)** Bonneville Power Administration, Portland, OR.

Post, J.R., and D.O. Evans. 1989. Experimental evidence of size-dependent predation mortality in juvenile yellow perch. Can. J. 2001. **67:521-523.**

Rand, **D.M,** and G.V. Lauder. 1981. Prey capture in the chain pickerel, <u>Esox nicer</u>: **correlatons** between feeding and locomotor behavior. Can. J. 2001. **59:1072-1078.**

Redding, J.M., C.B. Schreck, E.K. Birks, and R.D. Ewing. 1984. Cortisol and its effects on plasma thyroid hormone and electrolyte concentrations in fresh water and during seawater acclimation in yearling **coho** salmon, <u>Oncorhynchus kisutch</u>. Gen. and Comp. **Endocrin.** 56: 146-155.

Reeves, G.H., F.H. Everest, and C.E. **McLemore.** 1983. A recirculating stream aquarium for ecological studies. USDA Forest Service Research Note PNW-403. Pacific Northwest Forest and Range Experiment Station, Portland, OR. 8 p.

Rice, J. A., J. E. **Breck,** S. M. **Bartell** and J. **F. Kitchell.** 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environ. Biol. Fish. **9:263-275.**

Rice, J. A. and P. A. Cochran. 1986. Independent evaluation of a bioenergetics model for largemouth bass. Ecology. 65:732-739.

Rieman, B. **E.,** R. C. Beamesderfer, S. Vigg and T. P. Poe. 1988. Predation by resident fish on juvenile salmonids in a **mainstem** Columbia Reservoir: Part IV. Estimated total loss and mortality of juvenile salmonids to northern squawfish, walleye, and smallmouth bass. In: Poe, T. P. and B. **E.** Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts **DE-A179-82BP34796** and **DE-A179-82BP35097)** Bonneville Power Administration, Portland, OR.

Rondorf, D. W., M. S. Dutchuk, A. S. Kolok and M. L. Gross. 1985. Bioenergetics of juvenile salmon during the spring outmigration. Annual Report 1983, (Contract **DE-AI79-82BP35346),** Bonneville Power Administration, Portland, OR.

Rondorf, D.W., J.W. **Beeman,** J.C. Faler, M.B. Free, E.J. Wagner. 1989. Assessment of **smolt** condition for travel time analysis. Annual report to Bonneville Power Administration, Portland, Oregon (Contract number **DE-AI79-87BP35245).**

Schreck, C.B. 1981. Stress and compensation in teleostean fishes: response to social and physical factors. Pages **295-**321 **in** A.D. Pickering, editor. Stress and fish. Academic Press, London.

Sigismondi, L.A. and L.J. Weber. 1988. Changes in avoidance response time of juvenile chinook salmon exposed to multiple acute handling stresses. Trans. Am. Fish. **Soc. 117:196-201.**

Snedecor, G. W. and W. G. Cochran. 1980. Statistical Methods, Seventh Edition. The Iowa State University Press, Ames Iowa.

Sokal, R.R., and F.J. Rholf. 1981. Biometry, 2nd edition. Freeman Press, San Francisco.

Stein, R.A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. Ecology **58:1237-1253.**

Stewart, D. J. and **F.** P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: An energetics-modeling synthesis. Tran. Am. Fish. **Soc. 115:643-661.**

Stewart, D. J., J. F. **Kitchell** and L. B. Crowder. 1981. Forage fishes and their **salmonid** predators in Lake Michigan. Trans. Am. Fish. **Soc. 110:751-763.**

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An **energetics** model for lake trout, <u>Salvelinus pamavcush</u>: application to the Lake Michigan population. Can. J. Fish. **Aquat.** Sci. **40:681-698.**

Swenson, W. A. and L. L. Smith Jr. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (<u>Stizostedion vitreum vitreu</u>m). . Fish. Res. Bd. Canada **30:1327-1336.**

Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from **prey** populations? Ecology, **68:669-674.**

Thornton, K. W. and A. S. Lessen. 1978. A temperature algorithm for modifying biological rates. Trans. Am. Fish. **Soc. 107:284-287.**

Van Oosten, J. 1957. The skin and scales, p. 207-244. In: M. E. Brown **(ed.)** The physiology of fishes. Vol. 1. Academic Press, New York, NY.

Vigg, S. 1988. Functional response of northern sguawfish predation to **salmonid** prey density in **McNary** Tailrace, Columbia River. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts **DE-A179-82BP34796** and **DE-A179-82BP35097)** Bonneville Power Administration, Portland, OR.

Vigg, S. and C. C. Burley (Manuscript in Review). Temperature dependent maximum daily consumption of juvenile salmonids by northern sguawfish (<u>Ptvchoceilus oreaonenesis)</u> from the Columbia River.

Vigg, S., T. P. Poe, L. A. Prendergast, and H. **C.** Hansel, 1988. Predation by resident fish on juvenile salmonids in a **mainstem** Columbia River Reservoir: Part II. Consumption rates of northern squawfish, walley, smallmouth bass, and channel catfish. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts **DE-A179-82BP34796** and **DE-A179-82BP35097)** Bonneville Power Administration, Portland, OR.

Vigg, S. and L. A. Prendergast (Manuscript in preparation). Gonad development and spawning of northern sguawfish in a **mainstem** Columbia River reservoir.

Wahl, D.H. and R.A. Stein. 1988. Selective predation by three esocids: The role of prey behavior and morphology. Trans. Am. Fish. **Soc. 117:142-151.**

Webb, P.W.   1976.   The effect of size on the fast-start
    performance of   rainbow   trout **Salmo** aairdneri   and a
    consideration of piscivorous predator-prey interactions. J.
    Exp. Biol. **65:157-177.**

Webb, P.W. 1984a. Body and fin form and strike tactics of four
    teleost predators   attacking   fathead minnow **(Pimphales**
    promelas) prey. Can. J. Fish. Aquat. Sci. **41:157-165.**

Webb, P.W. 1984b. Chase response latencies of some telostean
    piscivores. Comp. Biochem. Physiol. **79A:45-48.**

Werner, E.E. and D.J. Hall. 1974. Optimal foraging and the size
    selection of **prey by** the bluegill sunfish **(Lepomis**
    macrochirus). Ecology **55:1042-1052.**

Winberg, G. G.   1956. Rate of metabolism and food requirements
    of fishes. Belorussian Univ., Minsk.   253 p.   (Transl. by
    Fish. Res. Bd. Can. Transl. Ser. No. 164, 1960).

Wright, L.D. 1970.   Forage size preference of the **largemouth**
    bass. Prog. Fish Cult. **32:39-42.**

Zar, J.H. 1984. Biostatistical **analysis.** Prentice-Hall, Inc.
    Englewood Cliffs, N.J.

APPENDIX A

Abstract

Maximum daily consumption rate (C_{max} as ration or number) of northern squawfish *(Ptychocheilus oregonensis)* from the Columbia River, increased exponentially **as** a function of temperature. Predator weight did not explain a significant independent proportion of variation in C_{max}. The mean maximum daily ration, determined *from* replicate *ad libitum* feeding on juvenile Pacific salmon *(Oncorhynchus spp.),* was 0.45, 0.67, 3.51, and 4.51 $cg \cdot g^{-1}$ at 8.0, 12.5, 17.0, and 21.5°C, respectively. To quantify the temperature dependent consumption relation for use in simulation modeling, replicate C_{max} data within the preferred temperature range were fit to exponential and exponential sigmoid models. Based on a knowledge of thermal relations of northern squawfish, hypothetical C_{max} data at temperature extremes were combined with our results; *this* enabled us to fit **gamma** and Thornton and **Lessem** (1978) models over the entire environmental temperature range (0-27°C) observed in the Columbia River.